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Selection of Forage and Avoidance of Predation Risk by Partially Migratory Mule Deer

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SELECTION FOR FORAGE AND AVOIDANCE OF PREDATION RISK BY PARTIALLY MIGRATORY MULE DEER

By

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ABSTRACT

Migration by ungulates has traditionally been thought of as a strategy that increases access to forage quality or reduces exposure to risk of predation, but the benefits of migration may be waning globally. In partially migratory populations, the persistence of both migrant and resident strategies is an intriguing ecological phenomenon, because migrants and residents often face contrasting fitness consequences. Partial migration is common in mule deer (*Odocoileus hemionus*), a species that has experienced widespread declines across the western United States during recent decades. Mule deer seldom switch between migratory strategies throughout their lifetime, which may make them less resilient to environmental change than more behaviorally plastic ungulate species. To indicate the mechanisms maintaining partial migration, we investigated how predation risk, forage quality, and habitat selection in relation to these factors varied between migrant and resident mule deer. First, we developed resource selection functions (RSFs) for wolves and mountain lions to estimate predation risk. Then, we modeled forage quality throughout mule deer summer ranges. We then compared forage quality (kcal/m^2) and predation risk in migrant and resident summer ranges of 3 partially migratory populations across Western Montana. We found no substantial differences in forage quality between migrant and resident summer ranges, and predation risk did not differ predictably between the 2 groups. We used RSFs to assess how home range (2^{nd} order) and within-home range (3^{rd} order) selection varied between migrants and residents. At the 2^{nd} order, neither migrants or residents selected forage or avoided wolf predation risk, but both groups avoided mountain lion predation risk. At the 3^{rd} order, both migrants and residents selected for forage and avoided wolf and mountain lion predation risk. Given their exposure to similar forage and risk conditions between groups, and similar habitat selection patterns, our results suggest that the benefits of a migrant strategy did not outweigh those of a resident strategy during our study. Within mule deer populations, partial migration may be maintained due to changes in the relative benefits of migration over time. Mule deer behavior was consistent across different ecosystem types and migratory strategies, suggesting a general mechanism for summer habitat selection may exist for mule deer in forested environments of the Northern Rockies.

TABLE OF CONTENTS

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A NOTE ON AUTHORSHIP

For the remainder of this thesis I use the collective "we" to acknowledge the conceptual, logistical, and analytical assistance of collaborators that went into this project.

LIST OF TABLES

LIST OF FIGURES

Chapter 1: Habitat Selection by Wolves and Mountain Lions in Western Montana

This chapter is formatted for submission to a peer-reviewed scientific journal with Drs. Chad Bishop, Mike Mitchell, and Nick DeCesare as coauthors.

ABSTRACT

1. Reliable predictions of predator distribution can help characterize the 'landscape of fear' for prey species, and can be invoked to explain prey behavior. Determining consistent patterns of habitat selection by predators across multiple populations can yield generalizable predictions of their distribution that accurately apply in a variety of ecological settings.
2. In the Northern Rockies of the United States, predators like wolves (*Canis lupus*) and mountain lions (*Puma concolor*) have been implicated in fluctuations or declines in populations of game species like elk (*Cervus canadensis*) and mule deer (*Odocoileus hemionus*), but the distribution of these predators and their effects on ungulate behavior are poorly understood in many parts of this region.
3. Our goal was to develop generalizable predictions of habitat selection by wolves and mountain lions across Western Montana. We hypothesized both predator species would select habitat that maximized their chances of encountering and killing ungulates like elk and deer, and that minimized their chances of encountering humans.
4. We assessed habitat selection by wolves and mountain lions during summer using within-home range resource selection functions (RSFs) for multiple populations. We tested how generalizable our estimates of habitat-use were by testing how well RSFs predicted the spatial distribution of out-of-sample wolf and mountain lion telemetry data from separate populations.

5. Selection for vegetation cover-types varied substantially among wolf populations. Nonetheless, our predictions of wolf distribution were highly generalizable across different populations. Wolves consistently selected for simple topography, suggesting their cursorial hunting behavior and preference for ungulate prey results in predictable space-use patterns across multiple ecosystem-types throughout Western Montana. Predictions of mountain lion distribution were less generalizable. Use of rugged terrain by mountain lions varied widely across ecosystem-types, likely because mountain lions preferred the habitat of alternate prey species between those areas.
6. We found that topographic features may serve as better proxies of predation risk by wolves than vegetation cover-types. Moreover, our findings suggest mountain lion habitat selection is highly variable across ecosystem-types, depending on prey communities in a region, and highlight how behavioral plasticity may contribute to their success as generalist predators.

INTRODUCTION

Predators affect ecosystems directly by killing prey, and indirectly by influencing prey behavior and distribution (Courbin et al. 2013, Winnie and Creel 2017). Through habitat selection, predators impose varying levels of risk towards prey across space, creating a "landscape of fear" for prey (Laundré et al. 2001). Prey may exhibit antipredator behavioral responses to risky places by altering their foraging behavior to avoid predation risk, which can have further indirect effects on ecosystems by altering vegetation communities (Fortin et al. 2005, Schmitz et al. 2005). Understanding habitat selection by predators allows prediction of their distributions under current and future environmental conditions (McLoughlin et al. 2010). Such predictions can be invoked to explain prey behavior, predator-prey interactions, and trophic dynamics.

Characterizing the realized niche of predators (i.e. the resources and limiting factors required for positive population growth rate in the presence of competitors; Hutchinson 1957) helps predict their habitat. We define habitat as areas in geographic space that harbor the set of biotic and abiotic features and conditions required for a species' persistence (Hirzel and Le Lay 2008). Developing niche-based predictions of predator habitat requires an understanding of how costly and beneficial environmental factors that regulate survival and reproduction influence predator behavior. Through this, generalizable predictions of habitat selection, or predictions that accurately predict species distribution across a wide range of environmental conditions (Vaughan and Ormerod 2005), can be developed. Testing how well predictions of habitat selection apply to multiple populations can indicate whether those predictions are valid estimates of predation risk across novel ecological conditions. Moreover, generalizable predictions of habitat selection can obviate the need to conduct new behavioral studies every time interest in a species' distribution arises in a new region (Guisan and Zimmermann 2000).

For hunted populations of carnivores, factors directly regulating fitness, like food and the risk of encountering humans, are effective for developing generalizable predictions of their distribution (Mitchell and Hebblewhite 2005, Randin et al. 2006). Unfortunately, direct measures of such ultimate factors, like prey density, are rare. Proxies that correlate with the probability of encountering and/or capturing prey, like vegetation cover-types and topographic features, may be used to understand predator behavior instead. For example, open, topographically simple areas may signify zones where cursorial predators like wolves (*Canis lupus*) can maximize opportunities to detect and give chase to prey (Atwood, Gese, and Kunkel 2009; Hebblewhite, Merrill, and McDonald 2005). Alternatively, dense vegetation and rugged terrain may serve as proxies for hiding cover where ambush predators like mountain lions (*Puma concolor*) are likely

to capture prey, given an encounter (Laundré and Hernández 2003, Holmes and Laundré 2006, Robinson et al. 2015, Blake and Gese 2016). Given these general patterns, researchers often assume certain vegetation cover-types are accurate proxies of predator distribution, without directly testing the relationship between those proxies and predator behavior (Rettie and Messier 2000, Ripple and Beschta 2006, Acebes et al. 2013, Riginos 2015). However, while the ultimate factors driving a predator species' distribution may stay the same across its range, the proximate habitat features it uses may vary as environmental factors like prey community composition change across ecosystem-types (Guisan and Zimmermann 2000, Randin et al. 2006), making generalizable predictions of predator distribution difficult. Hypothesizing a priori how proxies ultimately tie to the distribution of a species, then testing those hypotheses against location data from multiple populations, can increase generality of predictions of predator distribution (Mitchell et al. 2001).

Since the mid 1990's, wolves and mountain lions have increased in abundance and expanded their range within the Northern Rockies of the United States (Russell et al. 2012, Robinson et al. 2014, Proffitt et al. 2015, Montana Fish Wildlife and Parks 2018*a*, *b*). Concurrently, declines of ungulate populations like mule deer (*Odocoileus hemionus*) have occurred (Mule Deer Working Group 2019), and predators have been implicated as a potential cause of these declines (Musiani and Paquet 2004, Ordiz et al. 2013). Summer is a critical period in the annual life-history of ungulates in the Northern Rockies, as summer forage availability may regulate ungulate population growth rate (Cook et al. 2004), but forage acquisition by ungulates may be limited by wolf and mountain lion predation risk (Hebblewhite and Merrill 2009; Forshee 2018). However, the distribution of these predators and their effects on ungulate behavior are poorly understood in many parts of the Northern Rockies, prompting the need for

generalizable predictions of wolf and mountain lion distribution in the region (Ausband et al. 2010, Robinson et al. 2015, Eacker et al. 2016).

Wolves are pack-living, territorial carnivores, that primarily prey on elk (*Cervus canadensis*), mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), and moose (*Alces alces*) in the Northern Rockies (Metz et al. 2012). As cursorial hunters, wolves frequently select topographically simple terrain like valleys and drainage bottoms, where they can travel quickly and engage in prolonged pursuits of prey over long distances (Husseman et al. 2003, Bergman et al. 2006). Wolves will often select open vegetation cover-types that contain high quality forage for ungulates to increase their chances of encountering prey, and where it is easier to chase down prey (Mitchell and Hebblewhite 2005, Courbin et al. 2013). Wolf behavior is also shaped by human encounter risk, especially within hunted populations. Roads may signify increased risk of encountering hunters, trappers, or being hit by vehicles in some settings, but may also serve as beneficial routes for energetically efficient travel while hunting. Behavioral responses of wolves to roads may change with the density of roads in their population range (i.e. a 'functional response' in selection; Mysterud and Ims 1998; Muhly et al. 2019; Newton et al. 2017).

Mountain lions are typically solitary, territorial, stalking predators. As the most widely distributed land mammal (besides humans) in the western hemisphere, mountain lions are prey generalists and exhibit a high degree of behavioral plasticity across biomes (Weaver et al. 1996). In the Northern Rockies, mountain lions primarily prey on elk, mule deer, white-tailed deer, and bighorn sheep ([*Ovis canadensis*]; Sawyer and Lindzey 2002, Husseman et al. 2003, Elbroch et al. 2013). Mountain lions are unlikely to make a kill if they begin an ambush >25 m away (Holmes and Laundré 2006), so are heavily reliant on hiding cover for hunting. Mountain lions

often select structurally complex, rugged topography, that provides fine-scale hiding cover features like boulders and outcrops (Elbroch et al. 2013). However, mountain lions will also select dense vegetation cover-types like thick forests and riparian areas within topographically simple areas (Laundré and Hernández 2003, Dickson et al. 2005, Robinson et al. 2015, Blake and Gese 2016). Due to their preference for cover, mountain lions are typically avoidant of roads, but their response to roads is also highly variable across different ecosystems (Belden and Hagedorn 1993, Sweanor et al. 2000, Dickson et al. 2005).

Our goal was to approximate the landscape of fear for elk and deer in Western Montana by predicting habitat selection by wolves and mountain lions during summer across a spectrum of ecological conditions in the region. To do this, we investigated how factors associated with human encounter probability and the probability of encountering and/or capturing ungulate prey influenced wolf and mountain lion habitat selection. We hypothesized that wolves and mountain lions would select habitat that maximized their chances of encountering and killing ungulates like elk and deer, and that minimized their chances of encountering humans. We predicted wolves would select for valleys, drainages, and low slopes, as capture of ungulate prey is easier in these areas (Bergman et al. 2006), and would select areas with higher road densities to facilitate quick travel while hunting. Additionally, we predicted that wolves would select for open-canopy vegetation cover-types, since these areas are often selected by elk and deer (Ager et al. 2003, Proffitt et al. 2016). We predicted mountain lions would select forested drainages and steep, rugged terrain to improve hiding cover while stalking prey. We predicted mountain lions would avoid roads to reduce their chances of encountering humans, seeking areas with denser hiding cover instead, and that they would avoid open vegetation cover-classes, selecting forests where hiding cover is better instead (Table 1.1).

To predict habitat selection by wolves and mountain lions in Western Montana, we developed resource selection functions (RSFs) using Global Positioning System (GPS) collared animals. We developed separate, population-specific RSFs for wolves and mountain lions in multiple study areas across Western Montana that varied in prey community composition, dominant vegetation cover-types, and topographic complexity. To assess the generality of our RSFs, we applied each population-specific RSF to out-of-sample telemetry data from other regions and assessed their predictive performance.

DATA SOURCES

To predict habitat selection by wolves, we used GPS-collar data from packs in the Cabinet and Salish mountain ranges (Cabinet-Salish), the Rocky Mountain Front, and the Whitefish Range, MT. Wolf data were collected by Montana Fish Wildlife and Parks (MFWP) wolf specialists during the summers (June 1 – September 1) of 2015 — 2018. These consisted of 664 locations from 4 packs in Cabinet-Salish, 1,549 locations from 6 packs on the Rocky Mountain Front, and 509 locations from 3 packs in the Whitefish Range, totaling to 2,722 used locations. Within each study area, we developed a study-area specific RSF for wolves, then tested each study area-specific RSF on telemetry data from wolves in the other 2 study areas, respectively (Table 1.2).

To predict habitat selection by mountain lions, we used radiotelemetry data from collared mountain lions in 3 study areas: The Garnet Range, the Whitefish Range, and the Rocky Mountain Front. The Garnet data consisted of 40,831 GPS collar locations that uploaded during the summers of 2001 — 2006 from 17 mountain lions (14 females, 3 males) that were collared from 2001 — 2006 as part of a previous long-term study by Robinson and Desimone (2011). The Whitefish Range data consisted of 875 Very High Frequency (VHF) radiotelemetry collar locations from 34 mountain lions (25 females, 9 males) collected during summers 1992 — 1996

in a study by Kunkel et al. (1999). The Rocky Mountain Front data consisted of 145 VHF telemetry locations from 20 mountain lions (12 females, 8 males) collected during summers 1991 — 1992 in a study by Williams (1992). The Whitefish Range and Rocky Mountain Front data were insufficient for developing RSFs, so to predict mountain lion habitat selection across a spectrum of ecological conditions, we developed multiple RSFs for mountain lions using Garnet Range GPS collar data, and then tested their predictive performance on VHF collar data from the Whitefish Range and Rocky Mountain Front.

STUDY AREAS

The Garnet Range — The Garnet Range study area was 7,908 km^2. Elevations ranged from 1,160 m to 2,156 m (Figure 1.1). The Garnets were characterized by relatively moderate rolling topography, and primarily consisted of mesic forests and timber harvests. From 2001-2006, black bears (*Ursus americanus*), grizzly bears (*U. arctos*), coyotes (*Canis latrans*), and a single wolf pack in 2006 were sympatric with mountain lions in the Garnets (Robinson and DeSimone 2011). The ungulate community in the Garnets was composed of white-tailed deer, mule deer, elk, and moose. Local biologists believe white-tailed deer were the most abundant ungulate in the Garnets while mountain lion data were being collected, followed by mule deer, elk, and moose (S. Eggeman, MFWP Regional Wildlife Biologist, personal communication).

The Rocky Mountain Front — The Rocky Mountain Front encompassed 5,300 km^2, with elevations ranging from 1,240-2,800 m. The study area represents the transition zone between the Great Plains and the Rocky Mountains, and contained a pronounced east-to-west gradient in dominant vegetation cover classes, elevation, and topographic complexity. The eastern portion of the Rocky Mountain Front comprised open, relatively flat mixed grass prairie, and the western portion contained the mountains of the Bob Marshall Wilderness, consisting of steep, cliffy

terrain and comprising a patchy mosaic of burned areas, mesic conifer forests, meadows, and subalpine steppe. The Rocky Mountain Front is home to all of Montana's native ungulates (except bison [*Bison bison*]), including mule deer, white-tailed deer, elk, moose, bighorn sheep, mountain goats (*Oreamnos americana*), and pronghorn (*Antilocapra americana*), as well as a diverse suite of carnivores including wolves, mountain lions, coyotes, grizzly bears, black bears, and bobcats (*Lynx rufus*).

Cabinet-Salish — The Cabinet-Salish study area encompassed 5,200 km^2, with elevations ranging from 630-2,700 m. The study area was bisected by the Fisher River. The Salish Mountains in the eastern portion of the study area are characterized by moderate, rolling topography, and were primarily composed of mesic forests, grasslands, and timber harvests. The Cabinet Mountains in the west are steeper and more rugged than the Salish Mountains, and contained wetter forest transitioning upwards to subalpine areas. The Cabinet-Salish was home to the same carnivores and ungulate species as the Rocky Mountain Front, save for pronghorn.

Whitefish Range — The Whitefish Range study area encompassed 4600 km^2, with elevations ranging from 780-2,400 m. The mountains were dominated by wet and mesic conifer forests, and a smaller proportion of subalpine forest, open grasslands, burned areas, and timber harvests. The study area is bordered to the North by Canada and to the east by Glacier National Park. The Whitefish Range was home to the same carnivore and ungulate species as the Cabinet-Salish, save for mountain goats.

METHODS

Developing wolf RSFs

We developed 3rd order (within-home range) RSFs (Johnson 1980) for wolves using GPS-collar locations that uploaded between June 1 and September 1, 2014 — 2018. We began with 4,532 locations, but removed locations that likely uploaded while wolves were not traveling to focus on hunting behavior. To do this, we calculated step lengths and movement rates between each wolf location, and removed locations preceding steps with movement rates of <0.025 km/hr. using the 'amt' package (Signer et al. 2011) in R version 3.5.1 (R Core Team, 2018). This led to removal of 1,821 locations, so we analyzed 2,711 used locations in RSFs. With the reduced dataset, we constructed 95% kernel density estimate (KDE) home ranges for each individual wolf using the adehabitatHR package (Calenge 2006) in R, with 'href' as the smoothing parameter. For used samples, we included GPS locations that were within individual home ranges. For available samples, we randomly sampled 5 points per used location of an individual within that individual's home range (Aarts et al. 2012), totaling 13,610 available locations for wolves.

We tested the effects of variables that have previously been shown to correlate with prey encounter and kill probability (given an encounter), and risk of human encounter for wolves in RSFs. These included topographic (topographic position index [TPI], terrain ruggedness index [TRI], and slope), vegetative (vegetation cover-type and forest canopy cover) and anthropogenic (road density) variables (Table 1.1). TPI compares the elevation of a cell in a digital elevation model to the mean elevation of a specified neighborhood around that cell, and we specified a 1 km^2 window around each cell for our TPI raster. TRI calculated the mean of the absolute differences between elevation at a cell and the 8 surrounding cells of a $30m^2$ digital elevation model. To classify vegetation cover-types, we used a Montana state landcover map (MTNHP 2017) that we reclassified into 5 vegetation cover-classes: Riparian, Conifer forest, Grasslands/Shrublands, Timber harvests, and Burns. Cover-types that didn't fall into these

categories and composed <2% of the study area were classified as “Other”. We identified additional burns and harvests using disturbance maps from Montana Fish, Wildlife and Parks (MFWP) and LANDFIRE (LANDFIRE 2017). We categorized timber harvests as conifer forest in the Garnets, since we lacked timber harvest layers from this region.

To control for collinearity, we calculated the Pearson’s correlation coefficient (r) for each pair of variables we tested, and none were correlated with $r > 0.5$. We used fixed-effect logistic regression to develop a study area-specific RSF for wolves in the Rocky Mountain Front, Cabinet-Salish, and Whitefish study areas. For each study area, we developed a global model that included the full suite of variables and biologically interpretable two-way interactions. Conifer forest was the reference vegetation-cover type category in global models, since it was the most abundant cover type available within wolf and mountain lion home ranges. Continuous variables were centered on their mean and scaled in standard deviation units. We screened each global model for uninformative parameters by ranking each variable by level of importance (estimated as the absolute value of β/SE), then sequentially removed one variable at a time in ascending order of importance (Arnold 2010). If removal of a variable reduced Akaike’s Information Criteria (AIC) values, it was discarded from the model. If removal of a main effect increased AIC, but inclusion of that main effect in an interaction decreased AIC, the main effect and interaction were retained. We repeated this process until no additional variable could be removed without increasing AIC. To further control for multicollinearity, we calculated variance inflation factors (VIFs) for each variable and eliminated variables with VIF>5. We calculated 95% confidence intervals (CI’s) on the coefficients for each variable and eliminated variables whose CI overlapped zero from final models, unless the CI of a main effect overlapped zero but the CI of an interaction with that main effect did not.

We tested whether selection for roads by wolves changed as a function of road availability in each pack's territory using mixed-effects logistic regression. We combined GPS data from our 3 study areas for wolves and determined a top fixed-effects RSF for all packs using the same model selection procedures outlined above (Arnold 2010). Then, we added a random intercept for each pack and a random coefficient for the effect of roads to this model, and calculated separate pack-specific slope coefficients for the effect of roads on selection (Gillies et al. 2006). We converted coefficients to the odds scale, plotted the trend line between odds of selection for roads and mean road density in each pack's territory, and calculated the slope of this function, where a non-zero slope provided evidence for a functional response in selection of roads by wolves (Holbrook et al. 2019; Figure 1.2). In total, we developed 4 RSFs for wolves: 3 fixed-effects models (developed separately for the Cabinet-Salish, the Whitefish Range, and the Rocky Mountain Front) and 1 mixed-effects RSF for all study areas combined.

Developing mountain lion RSFs

Our goals when developing mountain lion RSFs were twofold: (1) develop a model using data from the Garnet Range that best explained mountain lion habitat selection within that study area, and (2) develop models using data from the Garnet Range that best predicted mountain lion distribution in the Whitefish Range and Rocky Mountain Front. We developed 3rd order RSFs for mountain lions in the Garnet Range, and included all locations that uploaded during summer in RSF analysis, because mountain lion habitat selection does not vary substantially with behavioral state (Blake and Gese 2016). We constructed 99% KDEs to estimate mountain lion home ranges, because 95% KDEs resulted in many non-contiguous portions of individual home ranges that those individuals returned to regularly, and we felt the area between those disjoint polygons should be included in individual home ranges (Kie et al. 2013). We used the same method for

sampling used and available locations for mountain lions as we did for wolves, totaling 40,831 used locations and 204,155 available locations for mountain lions in the Garnet Range. We tested the same variables and used the same model selection procedures as outlined above for wolves to develop an RSF that best explained mountain lion habitat selection within the Garnet Range. This RSF contained a quadratic effect of TRI, suggesting mountain lions in that study area selected for moderate topographic ruggedness. We will refer to this model as the "moderate ruggedness model".

To develop models that predicted mountain lion distribution in the Whitefish Range and Rocky Mountain Front, we visually inspected VHF telemetry locations from mountain lions in those study areas on a topographic map. We noticed mountain lions on the Rocky Mountain Front used steeper, more rugged terrain than in other study areas. Mean TRI at used locations of mountain lions on the Rocky Mountain Front ($\bar{x}$ = 80.882, SD = 30.299) was 1.76 times higher than mean TRI in the Whitefish Range ($\bar{x}$ = 45.85, SD = 43.266) and 1.22 times higher than mean TRI in the Garnet Range ($\bar{x}$ = 66.213, SD = 27.244). This prompted us to develop a second model with Garnet data that did not include the quadratic effect of ruggedness, which we will refer to as the "high ruggedness model". In total, we developed 2 fixed-effects RSFs for mountain lions using data from the Garnet Range: a "moderate ruggedness model" and a "high ruggedness model".

Testing generality of RSF predictions

We tested the fit of fixed-effects RSFs developed for wolves and mountain lions using internal 5-folds cross validation with the "kxvglm" package (Boyce 2002) in R. We binned the predictions of each RSF into 10 equal-area deciles, then calculated the spearman's rank correlation (r_s) between decile bin-rank (ranging from low relative predicted probability of use [1] to high

relative predicted probability of use [10]) and the proportion of used locations within each binned RSF decile (Figure 1.3; 1.4). For wolves, we tested the generality of fixed-effect RSFs on data from separate ecosystem-types by applying each study-area-specific RSF to out-of-sample data from the other 2 study areas, respectively, and examined fit using 5-folds cross validation (Boyce 2002). Again, we binned RSF predictions into 10 equal-area deciles and calculated r_s between decile bin-rank and the proportion of used locations in each binned RSF decile (Figure 1.3). For mountain lions, we tested how well the moderate and high ruggedness models predicted the relative probability of use at locations from VHF-collared mountain lions on the Rocky Mountain Front in the Whitefish Range. We binned these predicted RSF values into 10 equal-area deciles. We also calculated r_s between RSF decile bin-rank and frequency of use of each binned RSF decile (Figure 1.4).

RESULTS

Wolf RSFs

Across all study areas, wolves selected for valleys and drainages and low slopes (Table 1.3). Selection for vegetation cover-types varied by study area (Table 1.3). Grass/shrublands were avoided in Cabinet-Salish, but had no effect in the other 2 study areas. Wildfires were selected in the Whitefish Range and Rocky Mountain Front, but had no effect in Cabinet-Salish. Harvests were only selected on the Rocky Mountain Front. Selection for canopy cover and roads varied by study area. Wolves selected high canopy cover on the Rocky Mountain Front and Whitefish Range, but slightly avoided high canopy cover Cabinet-Salish, (Table 1.3). Wolves generally avoided roads in Cabinet-Salish and on the Rocky Mountain Front, but in the latter study area, they selected roads within high canopy cover areas. Wolves selected for roads in the Whitefish Range. Our multi-study area mixed-effects model provided modest evidence that selection for

roads increased as mean road density in a pack's territory increased. The mean effect of road density on selection across all packs was negative (β = -0.074, SE = 0.138), but varied from negative to positive between packs (β = -0.751 — 0.273). For every 1 km per km^2 increase in road density within a pack's territory, odds of selection for roads increased by 19.2% (P = 0.098; 95% CI = [-0.041 — 0.425]; Figure 1.2).

Wolf RSF generality

Study area-specific wolf RSFs performed well during internal model validation (r_s = 0.957 – 0.967). Study area-specific RSFs were highly generalizable as well. Mean r_s from models developed in other study areas and applied to testing data ranged from 0.912 — 0.988 (Figure 1.3).

Mountain Lion RSFs

The moderate ruggedness RSF, which best explained mountain lion habitat selection in the Garnet Range, included topographic position, road density, canopy cover, "Other" landcovers, terrain ruggedness (TRI) and a quadratic effect of TRI. Mountain lions in the Garnets selected valleys and drainages, but there was a positive interaction between topographic position and canopy cover, meaning mountain lions selected for ridgelines and peaks with high canopy cover. Mountain lions selected areas with higher canopy cover in general, and selected areas with moderate ruggedness, as indicated by the quadratic effect of TRI. Garnet mountain lions avoided roads. The high ruggedness RSF included the same covariates as the moderate ruggedness RSF, except for the quadratic effect of TRI. The effects of topographic position, road density, canopy cover, and "Other" landcovers were similar between the moderate ruggedness RSF and the high

ruggedness RSF. However, TRI had a strong positive effect in the high ruggedness model, so it predicted the distribution of lions that selected more rugged terrain.

Mountain lion RSF generality

Both the moderate ruggedness and high ruggedness RSFs performed well during internal validation in the Garnet Range (r_s = 0.952 and 0.939, respectively). In the Whitefish Range, the moderate ruggedness RSF performed well (r_s = 0.936; Figures 1.4 and 1.5), but the high ruggedness RSF performed poorly (r_s = -0.952; Figure 1.4). On the Rocky Mountain Front, the moderate ruggedness RSF performed poorly (r_s = -0.863; Figure 1.4), and the high ruggedness RSF performed better (r_s = 0.673; Figure 1.4 and 1.5).

DISCUSSION

Wolves selected for simple topography like valleys, drainages, and low slopes across all study areas, consistent with our predictions. This lends support to our hypothesis that wolves would select habitat to increase their chances of encountering/killing ungulates like elk and deer. Contrary to our predictions, selection for vegetation cover-types hypothesized to contain high quality ungulate forage was highly variable across study areas. In the Cabinet-Salish, wolves avoided open areas like burns, grasslands, and low canopy forest, but selected those vegetation cover-types in the other study areas. We found support for our hypothesis that wolves would select habitat that minimized their chances of encountering humans. As we predicted, wolves did select for roads, however, the strength of selection for roads depended on the probability of being detected by humans, given a road's location. On the Rocky Mountain Front, the majority of roads were located in open prairie, where vulnerability to human detection was high. Accordingly, wolves there avoided roads unless they were within forests. In contrast, packs in

the thickly-forested Whitefish Range all selected for roads (Figure 1.2), suggesting the benefit of easier travel in proximity to hiding cover outweighed the risk of encountering humans there. The density of roads in a pack's territory explained some of the variation in selection for roads, as packs in areas with high road densities not only used roads more (as would be expected even if habitat use were random), but also selected roads more strongly than packs with low road densities in their territory (Figure 1.2).

Preference for ungulate prey, and the limitations of cursorial hunting behavior, may explain why wolves primarily selected simple topography across varying ecological conditions in this study. Wolf diets are commonly dominated by ungulate prey like elk and deer across their range (Pimlott 1967, Fuller et al. 2003, Garrott et al. 2007, Watts and Newsome 2017), and in the Northern Rockies, these ungulates often seek refuge in steep, high-elevation terrain during summer (Atwood 2004, Creel et al. 2005, Mao et al. 2005), effectively reducing prey density within simpler topography. However, for every pursuit wolves engage in, they have a low probability of capturing prey (Pimlott 1967, Mech et al. 2001, Bergman et al. 2006, Macnulty et al. 2014), so simple topography that makes prey more vulnerable is often important for successful hunts (Bergman et al. 2006). Thus, increased prey vulnerability within simple topography may outweigh the costs of lower prey densities in those areas, explaining why valleys, drainages, and low slopes were consistent predictors of wolf distribution across varying ecological conditions in our study system. Despite substantial variation in how wolves selected vegetation cover-types, each of our study area-specific RSFs for wolves was highly generalizable to different ecological conditions, indicating that selection for structurally simple topography is a common mechanism influencing wolf distribution in the Northern Rockies. However, these RSFs approximate the average, population-level behaviors of wolves, and do not account for the

idiosyncratic hunting behaviors some individuals or packs can display. For example, certain wolf packs have been known to specialize on mountain goats (Fox and Streveler 1983, Coté et al. 1997), beavers ([*Castor canadensis*]; Latham et al. 2013), and bison (Macnulty et al. 2014). Though our RSFs showed that wolves primarily selected simple topography for capturing deer and elk, as generalists, wolves are certainly capable of exploiting a wider variety of terrain.

For wolves, selection of vegetation cover-types associated with higher forage quality for ungulates was inconsistent across regions, suggesting the risk of encountering wolves was decoupled from ungulate forage dynamics. This may relieve elk and deer from having to make tradeoffs between forage and security from wolves during summer. Rather, broad-scale avoidance of valleys and drainages may be a more effective way for ungulates to circumvent predation risk from wolves in Western Montana. Our findings serves as caution against using vegetation cover as proxies of predation risk for prey in ecological studies (Moll et al. 2017). If avoidance of certain vegetation cover-types by prey is assumed to be a predator avoidance strategy, ecosystem-wide processes like trophic cascades could be falsely inferred.

Consistent with our predictions, mountain lions in the Garnets avoided roads and selected forested drainages and areas with high canopy cover. These features offer hiding cover, lending support to our hypothesis that mountain lions would select habitat for stalking and capturing ungulates and avoiding humans. However, each of our mountain lion RSFs was not generalizable across all study areas, presumably because mountain lions preferred different prey species in each study area. While VHF telemetry data in the Whitefish Range were being collected in the early 1990's, white-tailed deer made up 87% (SE = 0.01) of winter mountain lion kills there (Kunkel et al. 1999). White-tailed deer prefer low to moderately rugged terrain and wooded drainages in that region (Dusek et al. 2006). Accordingly, our best-performing model there (the

moderate ruggedness model) predicted mountain lions to select habitat preferred by white-tailed deer (Figure 1.5A). In contrast, on the Rocky Mountain Front, Williams (1992) documented that summer and fall mountain lion kills consisted of white-tailed deer (27%), elk (22%), mule deer (15%), bighorn (4%) and other mountain lions, small mammals, or unknown species (47%). Within that region, mule deer, elk, and bighorn prefer higher, more rugged terrain than white-tailed deer (Knight 1970, Erickson 1972, Kasworm 1981, Williams 1992), and our best-performing model there (the high ruggedness model) predicted mountain lion use in those areas (Figure 1.5B). Thus, we suspect discrepancies in the predictive performance of our RSFs between study areas can be accounted for by differential selection for rugged topography by mountain lions in the Whitefish Range versus the Rocky Mountain Front. This may be a product of different prey bases for mountain lions in those regions.

The lack of generality in our mountain lion RSFs highlights how flexible mountain lion habitat selection is relative to the type of topography their prey are using. As ambush predators, mountain lions are reliant on hiding cover for stalking, but appear unconstrained by broad-scale topographic features, allowing them to exploit prey in either mountainous terrain or in riparian areas and valleys. Numerous studies have shown that mountain lions are able to exploit prey in a wide variety of settings, like bighorn sheep in cliffy, rugged terrain (Ross et al. 1997), guanacos (*Lama guanicoe*) in steppe (Elbroch and Wittmer 2013), and beaver in riparian areas (Lowry 2014). Given the plasticity of mountain lion behavior relative to topography, broad-scale topographic features make for unreliable predictors of mountain lion habitat selection across variable prey settings, and fine-scale hiding cover features may be more reliable predictors. This may explain why our predictions of distribution were less generalizable for mountain lions than for wolves (Kunkel et al. 2013).

Given their generality to multiple ecosystem-types, our RSFs for wolves can be used to predict the spatial distribution of predation risk from wolves faced by ungulates in Western Montana during summer. Our RSFs for mountain lions can be used to estimate predation risk within the Garnets, Whitefish Range, and Rocky Mountain Front. However, since we did not model mountain lion habitat selection directly in the Whitefish Range and Rocky Mountain Front, our predictions of distribution may not account for the true variability in mountain lion behavior in those regions. Further, knowledge of prey selection by mountain lions should be considered if these RSFs are to be extrapolated to novel regions in Western Montana.

Table 1.1 Variables tested in resource selection functions with hypothesized biological relevance and predicted effect on wolf and lion habitat selection.

Variable	Wolves					Mountain lions					Data source
	Hypothesis[A]			Prediction[B]	Reference	Hypothesis			Prediction	Reference	
	Encounter	Kill	Risk			Encounter	Kill	Risk			
Road density (km/km^2)	+	0	+	Select high road densities to increase prey encounters	Kittle et al. 2015; Dickie et al. 2017; Muhly et al. 2019	+	0	+	Avoid high road densities to avoid humans	Dickson et al. 2005	Road density shapefile (MTNHP 2017)
Terrain Ruggedness Index (TRI)						-	+	0	Select high ruggedness for stalking prey	Kunkel et al. 2013; Robinson et al. 2015	terrain function from 'Raster' package (Hijmans et al. 2019)
Topographic Position Index (TPI)	0	+	0	Select valleys to chase down and kill prey	Atwood et al. 2009; Kunkel et al. 2013	0	0	0	Indifferent to valleys	Atwood et al. 2009; Kunkel et al. 2013	tpi function from 'SpatialEco' package (Evans 2018)
Slope	+	+	0	Select low slopes for easier travel and to chase down and kill prey	Hebblewhite et al. 2005						terrain function (Hijmans et al. 2019)
Canopy cover (%)	-	-	-	Select low canopy cover to increase encounters with prey	Hebblewhite et al. 2005	-	+	-	Select high canopy cover for stalking prey	Blake and Gese 2016	MOD44B percent tree cover raster, 250m resolution
Timber harvests	+	0	0	Select harvests to encounter prey	Hebblewhite et al. 2005	+	0	0	Indifferent to harvests	Blake and Gese 2016	LANDFIRE disturbance layer (https://www.landfire.gov/)
Grasslands & shrublands	+	0	0	Select grasslands to encounter prey		+	0	0	Indifferent to grasslands	Blake and Gese 2016	LANDSAT-derived Montana landcover map (MTNHP 2017)
Burns	+	0	0	Select burns to encounter prey	Hebblewhite et al. 2005	+	0	0	Indifferent to burns	Blake and Gese 2016	LANDFIRE & MTNHP

[A] "Encounter" column represents the relationship between habitat feature and the probability of encountering prey; + means positive effect, - means negative effect, 0 means no effect. "Kill" column represents the relationship to probability of killing prey, given an encounter. "Risk": relationship to probability of encountering humans.
[B] Predicted predator selection response

Table 1.2 Sources of radiocollar telemetry data used for developing RSFs, data used for testing those models in within-sample (internal) and out-of-sample (external) cross-validation, and years radiocollars were deployed on wolves and mountain lions in 4 total study areas throughout Western Montana.

Species	Model development data	Model testing data	
		Internal	External
Wolves	Cabinet/Salish[GPS]; 2015-2018 (MFWP)	Cabinet/Salish[GPS]	Whitefish Range[GPS] Rocky Mtn. Front[GPS]
Wolves	Whitefish Range[GPS]; 2015-2018 (MFWP)	Whitefish Range[GPS]	Cabinet/Salish[GPS] Rocky Mtn. Front[GPS]
Wolves	Rocky Mtn. Front[GPS]; 2015-2018 (MFWP)	Rocky Mtn. Front[GPS]	Whitefish Range[GPS] Cabinet/Salish[GPS]
Mountain lions	Garnet[GPS]; 2001-2006 (Robinson and DeSimone 2011).	Garnet[GPS]	Rocky Mtn. Front[VHF]; 1991-1992 (Williams 1992) Whitefish Range[VHF]; 1992-1996 (Kunkel et al. 1999)

[VHF] Locations from Very High Frequency-radiocollared animals.

[GPS] Locations from Global Positioning System-radiocollared animals.

Table 1.3 Logistic regression parameters, standard errors, (SE) and odds ratios from top-ranked fixed effects and mixed-effects resource selection functions for wolves and mountain lions.

Model	Parameter	Estimate	SE	Odds ratio	Lower 95% CI	Upper 95% CI
Wolves, Cabinet-Salish[F]	Road density	-0.107	0.037	0.899	0.836	0.965
Wolves, Cabinet-Salish[F]	Canopy cover	-0.007	0.003	0.993	0.986	0.999
Wolves, Cabinet-Salish[F]	Grass-shrublands	-0.363	0.181	0.695	0.482	0.983
Wolves, Cabinet-Salish[F]	TPI[A]	-0.012	0.001	0.988	0.985	0.990
Wolves, Cabinet-Salish[F]	Slope	-0.058	0.005	0.944	0.934	0.954
Wolves, Cabinet-Salish[F]	Grass-shrublands * TPI	0.012	0.004	1.012	1.004	1.021
Wolves, Rocky Mtn. Front[F]	Road density	-0.458	0.123	0.633	0.342	0.482
Wolves, Rocky Mtn. Front[F]	Canopy cover	0.001	0.002	1.001	0.997	1.005
Wolves, Rocky Mtn. Front[F]	Harvested forest	0.590	0.165	1.805	1.300	2.479
Wolves, Rocky Mtn. Front[F]	Other landcovers	0.463	0.097	1.589	1.312	1.922
Wolves, Rocky Mtn. Front[F]	Wildfire	0.383	0.065	1.467	1.292	1.666
Wolves, Rocky Mtn. Front[F]	TPI	-0.009	0.001	0.991	0.989	0.993
Wolves, Rocky Mtn. Front[F]	Slope	-0.065	0.004	0.937	0.931	0.944
Wolves, Rocky Mtn. Front[F]	Road density * canopy cover	0.008	0.003	1.008	1.002	1.014
Wolves, Whitefish Range[F]	Road density	0.230	0.055	1.259	1.131	1.401
Wolves, Whitefish Range[F]	Canopy cover	0.013	0.004	1.013	1.005	1.021
Wolves, Whitefish Range[F]	Wildfire	0.343	0.142	1.408	1.063	1.856
Wolves, Whitefish Range[F]	TPI	-0.012	0.002	0.988	0.984	0.992
Wolves, Whitefish Range[F]	Slope	-0.055	0.007	0.946	0.934	0.958
Wolves, Global Model[M]	Road density	-0.074	0.138	0.928	0.709	1.217
Wolves, Global Model[M]	Canopy cover	0.012	0.002	1.012	1.009	1.015
Wolves, Global Model[M]	Other landcovers	0.260	0.071	1.297	1.128	1.491
Wolves, Global Model[M]	Wildfire	0.742	0.054	2.101	1.892	2.334
Wolves, Global Model[M]	TPI	-0.010	0.001	0.990	0.989	0.992
Wolves, Global Model[M]	Slope	-0.068	0.003	0.935	0.930	0.940
Wolves, Global Model[M]	Road density * canopy cover	-0.002	0.001	0.998	0.995	1.000

Table 1.3 (continued).

Model	Parameter	Estimate	SE	Odds ratio	Lower 95% CI	Upper 95% CI
Wolves, Global Model[M]	Random intercept of pack	Variance 0.116				
Wolves, Global Model[M]	Random intercept road density*pack	Variance 1.116				
Wolves, Global Model[M]	Random slope of road density*pack	Variance 0.141				
Lions, Garnets, Moderate ruggedness[F]	TPI	0.002	< 0.001	1.002	1.002	1.003
Lions, Garnets, Moderate ruggedness[F]	Road density	-0.072	0.006	0.931	0.919	0.943
Lions, Garnets, Moderate ruggedness[F]	TRI[B]	0.009	< 0.001	1.009	1.009	1.010
Lions, Garnets, Moderate ruggedness[F]	TRI^2	-0.141	0.005	0.869	0.860	0.877
Lions, Garnets, Moderate ruggedness[F]	Canopy cover	0.007	< 0.001	1.007	1.007	1.008
Lions, Garnets, Moderate ruggedness[F]	Other landcovers	-0.289	0.024	0.749	0.714	0.785
Lions, Garnets, Moderate ruggedness[F]	TPI * canopy cover	< 0.001	< 0.001	1.000	1.000	1.000
Lions, Garnets, High ruggedness[F]	TPI	0.003	< 0.001	1.003	1.003	1.003
Lions, Garnets, High ruggedness[F]	Road density	-0.074	0.006	0.929	0.917	0.941
Lions, Garnets, High ruggedness[F]	TRI	0.005	< 0.001	1.005	1.005	1.005
Lions, Garnets, High ruggedness[F]	Canopy cover	0.009	< 0.001	1.009	1.009	1.010
Lions, Garnets, High ruggedness[F]	Other landcovers	-0.276	0.024	0.759	0.724	0.796
Lions, Garnets, High ruggedness[F]	TPI * canopy cover	< 0.001	< 0.001	1.000	1.000	1.000

[F] Fixed-effects only model

[M] Mixed-effects model

[A] Topographic Position Index

[B] Terrain Ruggedness Index

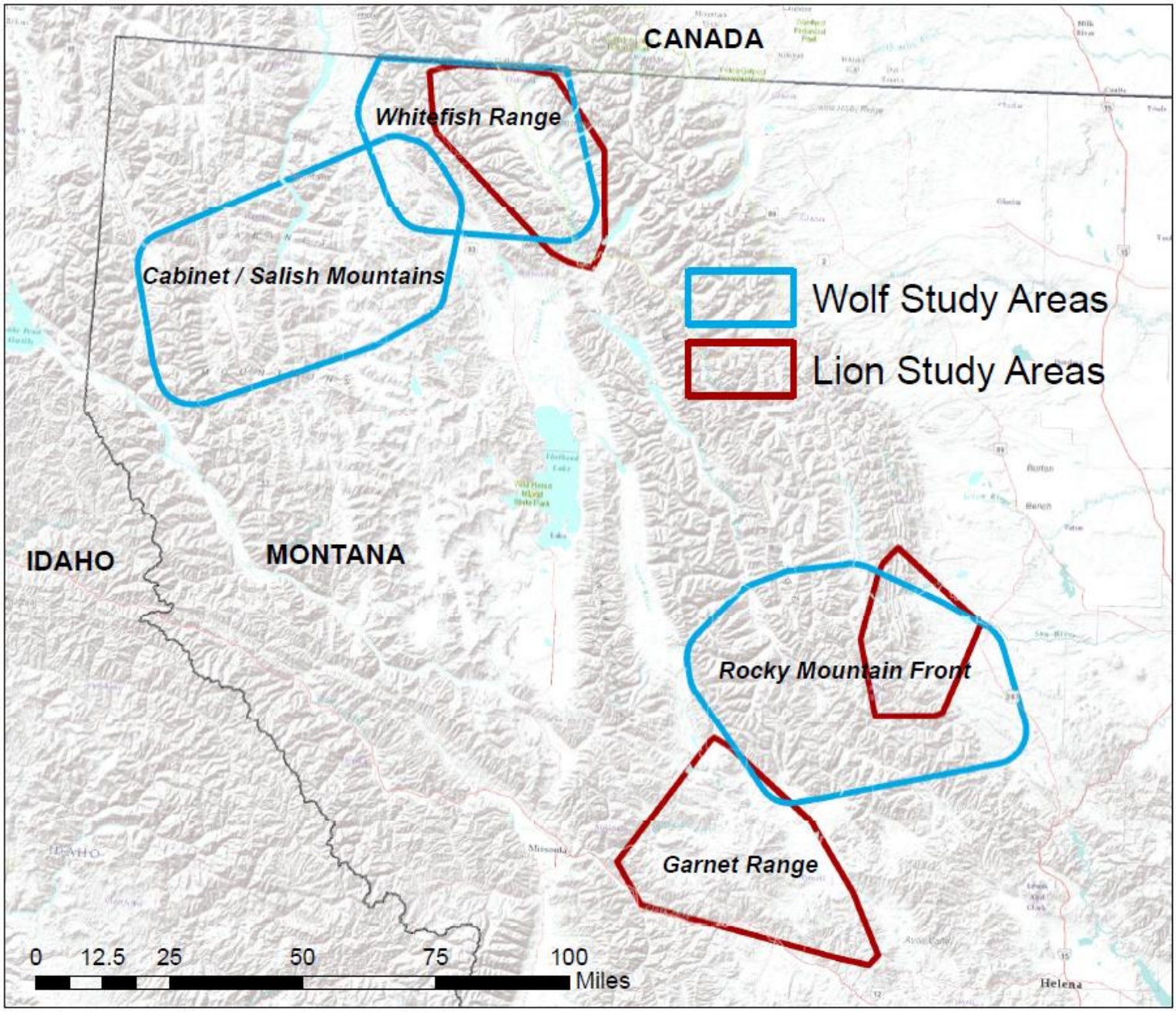

Figure 1.1 Wolf and mountain lion study areas. Polygons are 100% minimum convex polygons (MCPs) of wolf or lion GPS or VHF summertime collar locations that were used for RSF modelling and testing.

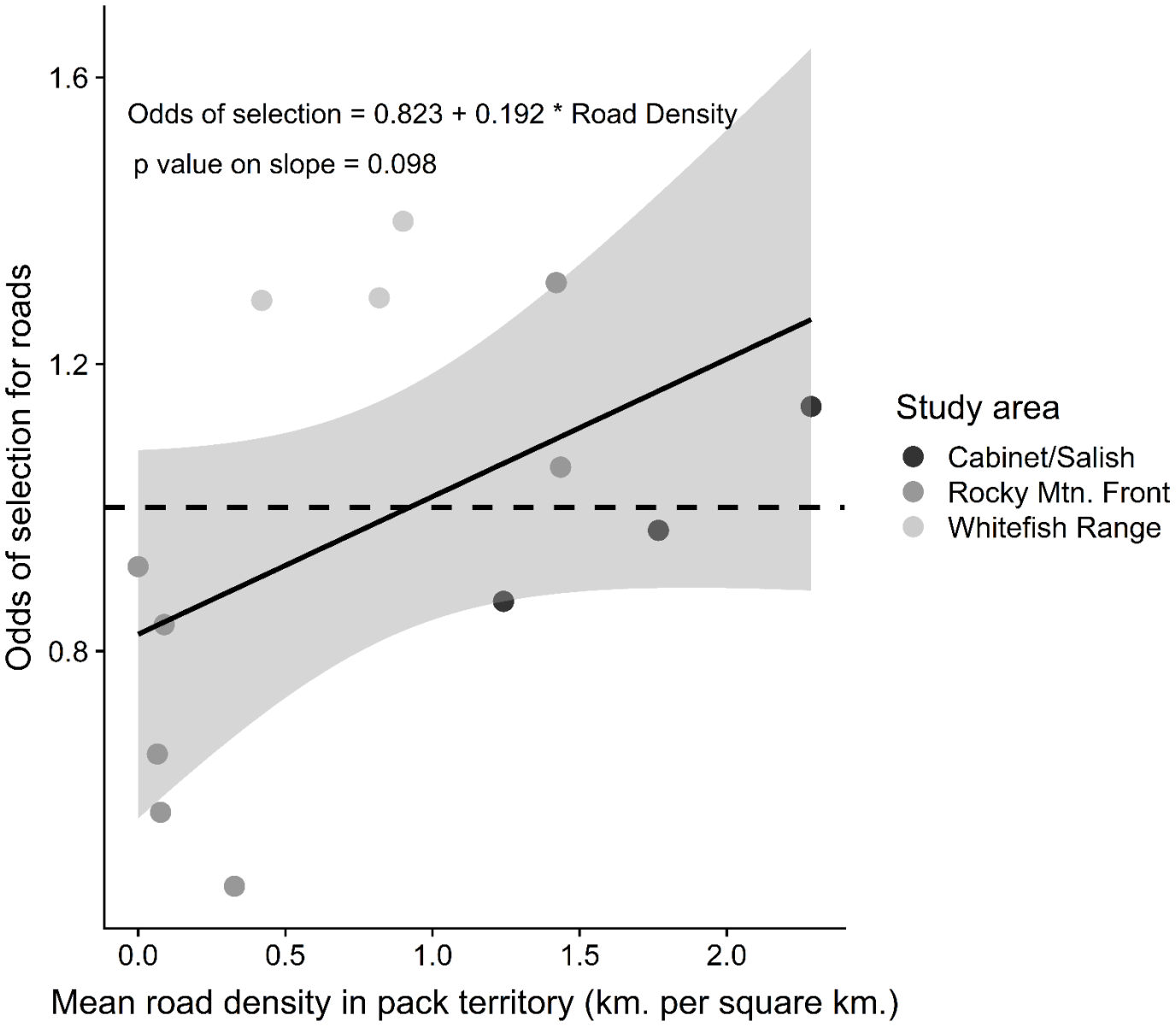

Figure 1.2. Odds ratios for the random effect of road density by pack from mixed effects logistic regression model of within-home range resource selection by wolves, plotted against mean road density in each pack's territory. Dashed line at y = 1 indicates neutral selection.

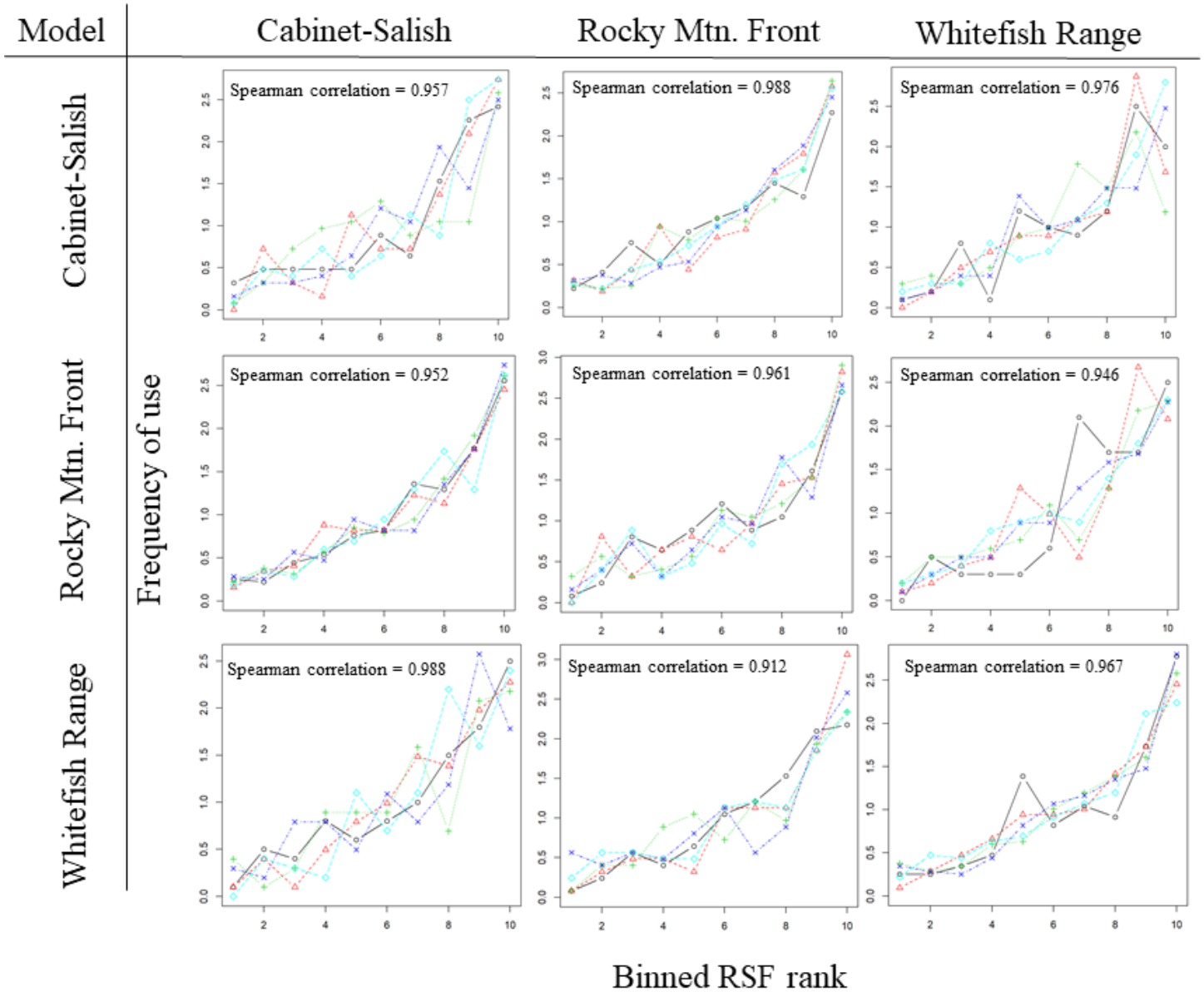

Figure 1.3. Number of locations used by wolves (y axis) per binned RSF decile (x axis) from fixed-effect logistic regression models developed with GPS collar data from wolves. Rows indicate the study area in which data to develop each model originated, and columns indicate the study area in which data to test each model originated. Each line in these plots represents 1 out of 5 folds of data used to cross-validate RSF predictions. Binned RSF ranks were estimated by predicting each RSFs across study areas, then binning predictions into deciles, where 0 = lowest predicted probability of use and 10 = highest predicted probability of use. Spearman correlations were calculated between each decile bin rank and the proportion of used locations in each bin.

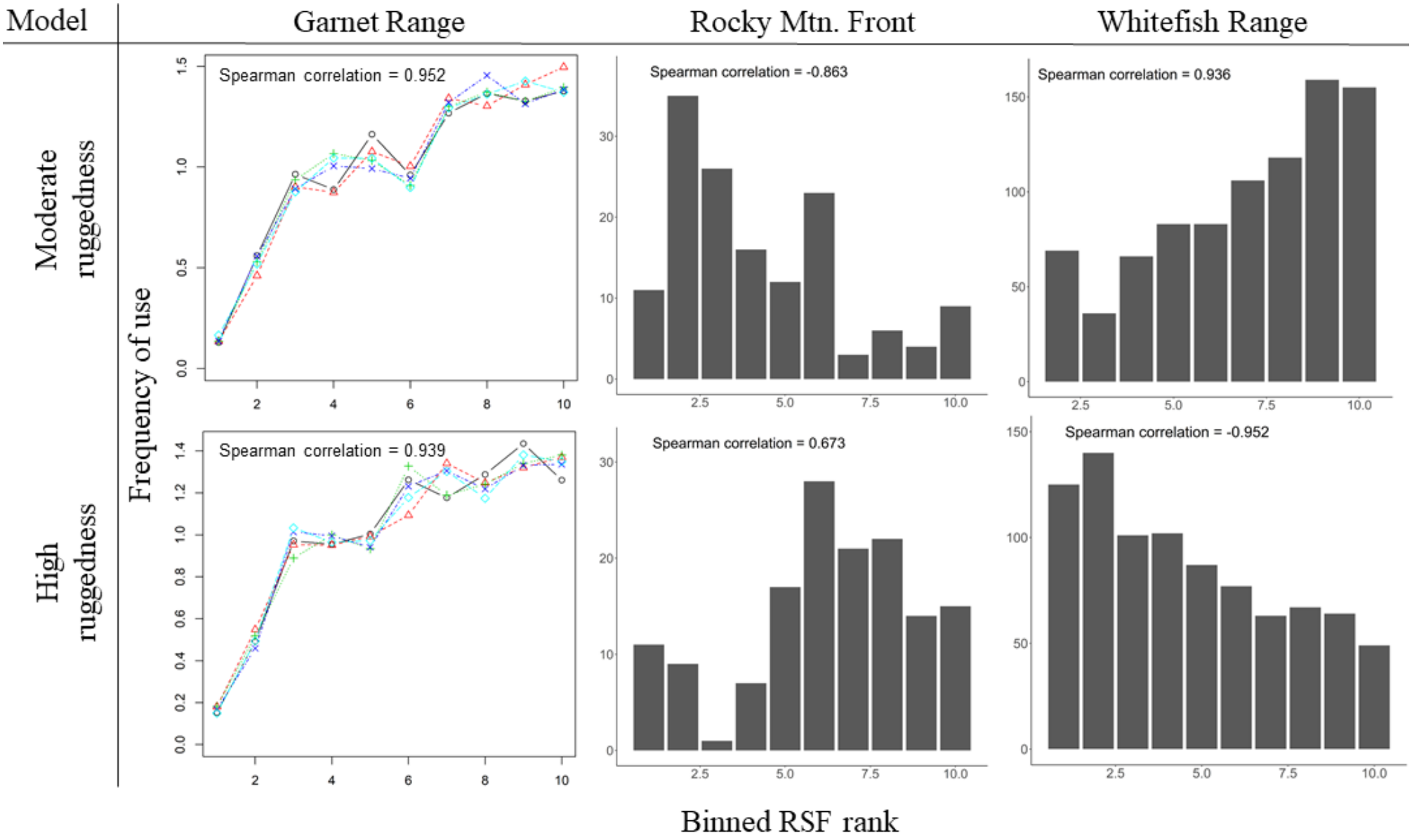

Figure 1.4. Number of locations used by mountain lions (y axis) per binned RSF decile (x axis) from fixed-effect logistic regression models developed with GPS collar data from mountain lions. Rows indicate different RSFs developed with Garnet Range GPS collar data, and columns indicate the study area in which data to test each RSF originated. In the Garnet Range plots, each line in plots represents 1 out of 5 folds of data used to cross-validate RSF predictions internally. In the Whitefish and Rocky Mtn. Front, VHF collar data used for testing RSFs were not split into folds.

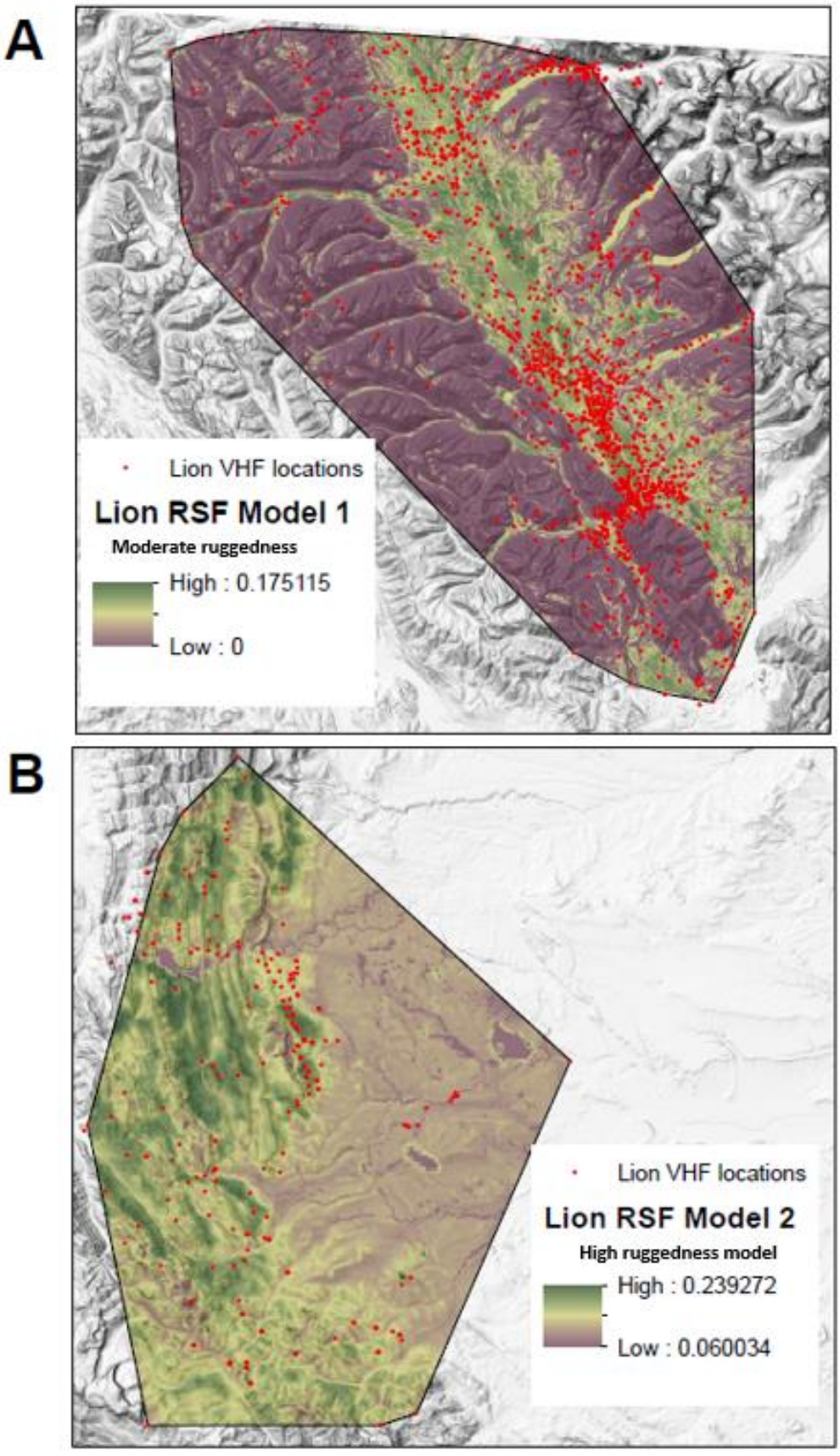

Figure 1.5. Predicted relative probability of use from **(A**) 'moderate ruggedness' mountain lion RSF in the Whitefish Range (Model 1), and **(B)** 'high ruggedness" mountain lion RSF (Model 2) on the Rocky Mountain Front. RSF models were tested on VHF telemetry data from Kunkel et al. (1999) and Williams (1992).

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Chapter 2: Consequences of Migratory Strategy on Habitat Selection by Mule Deer

This chapter is formatted for submission to a peer-reviewed scientific journal with Teagan Hayes and Drs. Chad Bishop, Mike Mitchell, and Nick DeCesare as coauthors.

ABSTRACT

1. In highly seasonal environments, ungulates can access different forage conditions and avoid predation risk in summer range by migrating. Within partially migratory populations, resource availability can vary substantially between migrants and residents. Migratory strategy can affect subsequent selection for forage and avoidance of predators at multiple spatial scales. Patterns of resource availability and selection between migrants and residents can help inform how partial migration persists in populations. Behavioral tradeoffs between forage and predation risk may vary as a function of forage availability in an area too.
2. To indicate mechanisms of partial migration's persistence in mule deer (*Odocoileus hemionus*) populations, we assessed how forage availability and risk from predators varied between migrant and resident summer ranges in 3 populations across Western Montana, and evaluated how mule deer selected habitat in relation to those factors. We hypothesized that migrants would have higher quality forage available to them than residents, and that residents would obtain adequate forage by selecting more strongly for forage at fine spatial scales than migrants. Further, we hypothesized that as forage availability increased at a given spatial scale, mule deer would forego selection of forage and show stronger avoidance of predators at a subsequently finer scale.
3. We estimated the availability of forage quality (in kcal/m^2) and predation risk from wolves (*Canis lupus*) and mountain lions (*Puma concolor*) between summer ranges of

migrant and resident mule deer. We compared the availability of forage quality and predation risk on summer ranges of migrants and residents mule, then assessed how selection for forage and avoidance of risk at the home range (2nd order) and within-home range (3rd order) scales varied across a range of forage availability.

4. Migrants and residents had similar forage quality available to them within each study area. At the 2nd order, neither migrants or residents selected forage or avoided wolf predation risk, but did avoid mountain lion predation risk. At the 3rd order, both migrants and residents selected forage and avoided wolf and mountain lion predation risk. Among individual home ranges, increased forage availability led to weaker 3rd order selection for forage and slightly weaker avoidance of mountain lion predation risk, and did not influence avoidance of wolves.
5. Given similar forage and predation risk conditions between migrant and resident summer ranges, and that migrants and residents selected these factors similarly at finer spatial scales, we rejected our hypothesis that migration exposes mule deer to higher quality forage. Rather, our findings suggest that partial migration is maintained in mule deer populations due to changes in the relative benefits of migration over time. Patterns of selection for forage and security by mule deer were highly consistent across different ecosystem types too, suggesting that avoidance of their most lethal predator (mountain lions) at broad scales, then selection of forage within home ranges, may represent a general mechanism for summer habitat selection by mule deer in forested environments of the Northern Rockies.

INTRODUCTION

In highly seasonal environments, forage quality and security from predation are important

resources that influence ungulate behavior and distribution (Bowyer et al. 2005, Bergman et al. 2015, Winnie and Creel 2017). Ungulate migration has traditionally been viewed as a strategy that increases access to forage or reduces exposure to predation risk during summer (Fryxell and Sinclair 1988). However, global declines in populations of migratory ungulates in the last century suggest that the benefits of migration may be waning (Harris et al. 2009). Partially migratory populations, in which some individuals migrate seasonally and others remain resident in the same range year-round (Chapman et al. 2011), offer the opportunity to study the relative benefits of migratory versus non-migratory behavior. The persistence of partial migration in populations is an intriguing ecological phenomenon, because the long-term fitness consequences of migrant and resident strategies should, in theory, be balanced (Lundberg 2013), but the benefits of one strategy often exceed those of the other (Nicholson et al. 1997, Schuyler et al. 2019). Multiple mechanisms have been hypothesized for how partial migration persists (Berg et al. 2019), each of which are associated with different patterns of resource availability and selection between migrants and residents.

Partial migration is thought to be maintained in populations through demographic balancing between migrant and resident strategies (Lundberg 2013). This balancing could be achieved when migrant and resident groups experience alternate benefits and costs. For example, migrants may gain access to higher quality forage than residents, increasing their reproductive success, but may be exposed to higher predation risk, reducing their probability of survival. Residents may face lower forage but lower risk than migrants, reducing their reproduction but increasing their survival, which could lead to similar long-term population growth rates of migrants and residents (Hebblewhite et al. 2011). Alternatively, if the availability of forage is lower and risk is higher for residents than for migrants, residents may be able to acquire similar

resources as migrants through fine-scale resource selection. Hebblewhite and Merrill (2009) observed this mechanism in a partially migratory population of elk, where residents faced low forage quality and high risk of wolf predation in their summer range, but exploited areas of high forage and low risk near human activity centers within their home ranges, enabling both migrant and resident strategies to persist. Further, if the benefits of one strategy are equal to or exceed the benefits of the alternate strategy, this could reflect a scenario where the relative benefits of migration are changing over time. Stochastic climate events (Middleton et al. 2013) or land-use changes (Barker et al. 2019) may alter the relative benefits of migration in a given year, but over a multi-year time scale, the benefits of each strategy may balance out. If this is the case, forage and risk conditions may not vary substantially between migrants and residents during a given year, and individuals of both strategies may select those factors similarly.

Partial migration is common in mule deer (*Odocoileus hemionus*) populations, but unlike most ungulates, individual mule deer show very little plasticity in whether or where they migrate on an annual basis (Sawyer et al. 2019). Therefore, mule deer may be less resilient to environmental change than more behaviorally plastic species like elk (*Cervus canadensis*; White et al. 1987, Brown 1992, Eggeman et al. 2016, Barker et al. 2019, Sawyer et al. 2019). Mule deer populations have declined throughout their range over the past 3 decades (Monteith et al. 2014), so conservation of habitat on their existing seasonal ranges is particularly important for the long-term viability of declining populations. Understanding resource selection by partially migratory mule deer is important because it could indicate how partial migration is maintained in an ungulate where individual migratory strategies are relatively fixed, and could indicate which resources should be prioritized for conservation of habitat for mule deer (Rettie and Messier 2000, Gaillard et al. 2010).

Accessing high-quality forage during summer is critical for mule deer because it strongly influences over-winter survival (Hurley et al. 2014). Anthropogenic habitat change has altered the availability of forage during summer for mule deer in some areas, contributing to populations declines (Sawyer et al. 2017). Predation risk can also affect mule deer populations indirectly by affecting their behavior, preventing access to high quality foraging areas and exacerbating the effects of decreased foraging opportunities (Atwood et al. 2009, Dwinnell et al. 2019). Within the Northern Rockies of the United States, wolves (*Canis lupus*) and mountain lions (*Puma concolor*) have undergone range expansion and population growth concurrently with changes in forage availability and mule deer declines (Russell et al. 2012, Robinson et al. 2014, Proffitt et al. 2015, Montana Fish Wildlife and Parks 2018*a*, *b*). Detailed studies are needed to parse out the relative effects of forage quality, predation risk, and their effects on mule deer behavior and distribution.

To assess the consequences of migratory strategy, habitat selection should be assessed at multiple spatial scales to reveal behaviors aimed at acquiring food or avoiding predators (Boyce 2006). Different scale-specific behaviors may arise between individuals in different ecosystem types, or with different migratory strategies that experience vastly different levels of forage availability on summer range (Guisan and Zimmermann 2000, Mauritzen et al. 2003, Godvik et al. 2009). Whether an individual does or does not migrate can influence how much forage is available to it at broad spatial scales (Dingle and Drake 2007) which can influence how forage is selected and predators are avoided at finer scales (e.g. the home range [2nd order] and within-home range [3rd order] scales; Johnson 1980; Mysterud and Ims 1998, Hebblewhite and Merrill 2009).

To indicate the mechanisms through which partial migration persists in mule deer populations, we evaluated how forage availability and predation risk from wolves and mountain lions varied between migrant and resident mule deer summer ranges, then assessed how mule deer selected those resources at finer spatial scales. We developed 3 alternate hypotheses to explain variation in resource availability between migrant and resident ranges: (1) *Forage-security tradeoff* — migrants will have high forage quality (in kcal/m^2) and predation risk from wolves and mountain lions within their summer range, whereas residents will have low forage quality and low risk, maintaining a demographic balance between strategies (Hebblewhite et al. 2011). If true, we predicted migrants would have higher forage quality (in kcal/m^2) and higher risk within their summer range than residents, but that both migrants and residents would select those factors similarly. (2) *Fine-scale resource compensation* — residents will have lower forage quality and higher risk in their summer range than migrants. If true, we predicted residents would select for forage and avoid risk at finer scales (i.e. 2nd or 3rd order) in a manner that achieves similar resource acquisition as migrants (Hebblewhite and Merrill 2009). (3) *Resource parity* — migrants and residents will have similar forage and risk conditions available within their summer ranges. If true, both migrants and residents would select resources similarly at the 2nd and 3rd order, acquiring similar levels of forage and security. This outcome could indicate a situation in which the benefits of each migratory strategy are currently similar, but that changes in the relative benefits of each strategy may occur over longer time scales than we were able to detect in our study (Middleton et al. 2013).

To determine how ecological context influenced how migrants and residents behave relative to forage and predation risk, we evaluated how 2nd and 3rd order selection for those factors varied across a spectrum of forage availability levels. We hypothesized that as forage

availability increased at a given spatial scale, mule deer would be free to forego selection of forage and minimize risk at a subsequently finer scale. If true, we predicted that in ecosystems with high forage quality, mule deer would show strong 2nd order avoidance of risk and weak selection for forage. Further, among individuals, those with high forage quality in their home ranges would show strong 3rd order avoidance of risk and weak selection for forage.

To test our hypotheses, we quantified the availability of forage quality and wolf and mountain lion predation risk during summer across three partially migratory mule deer populations in different ecosystem-types throughout Western Montana. To test how resource availability varied between migrants and residents, we compared how forage and predation risk differed between migrant and resident summer ranges in each population. To assess how migrants and residents behaved relative to forage and predation risk, and how environmental context influenced these behaviors, we used RSFs to model mule deer habitat selection at the 2nd and 3rd order and assessed how forage availability influenced selection for forage avoidance of risk at each of these scales.

STUDY AREAS

Our research took place in the Rocky Mountain Front/Bob Marshall Wilderness Complex (Rocky Mountain Front), the Cabinet and Salish mountain ranges (Cabinet-Salish), and the Whitefish Range (see study area descriptions, Chapter 1, page 8).

METHODS

Collecting locations of mule deer

To determine how resource availability and selection varied between migratory strategies and ecosystem-types, we deployed GPS collars (90 Lotek LifeCycle 330 collars and 12 Lotek

LifeCycle Pro 330 collars) on 136 female mule deer throughout our 3 study areas during winters of 2017-2019, and collected GPS collar data through autumn 2019. We targeted adult females to concurrently monitor adult female survival and fecundity as components of separate studies concerning deer population dynamics (Bishop et al. 2009, Forrester and Wittmer 2013). We collared 42 deer in the Cabinet-Salish, 49 in the Rocky Mountain Front, and 45 in the Whitefish Range. We captured mule deer using helicopter net-gunning, clover trapping, and ground-darting, and attempted to spread the locations of captures throughout population winter ranges. Capture protocols were approved by the University of Montana Institutional Animal Care and Use Committee (Animal Use Protocols 001-17CBWB-011017 and FWP03-2016). For resource selection analyses, we filtered our data to include only locations that uploaded between June 1-August 31, 2017-2019, which eliminated locations from 25 deer that died prior to June 1. We excluded 4 deer for which we were unable to retrieve spatial environmental data due to migration paths into Canada for summer. We further filtered data to include only individuals whose collars uploaded at least 30 locations during a given summer. After these screening procedures, the data we used for habitat selection modeling contained 68,318 locations for 171 animal-seasons from 100 individual deer.

Classifying deer into migratory strategies

We used net squared displacement (NSD; Bunnefeld et al. 2011) to classify individual mule deer summer movement behaviors into either migrant or resident categories. NSD measures the straight-line distance between an animal's starting point and subsequent daily locations. We used the migrateR package (Spitz et al. 2017) in Program R version 3.6.1 (R Core Team 2019) which uses a model-based approach to classify movement behaviors (Appendix C).

Comparing forage and risk in migrant and resident ranges

Delineating landscape-scale summer ranges for migrants and residents — Partial migration reflects a phenomenon whereby migrants and residents use different summer ranges at the landscape-scale (Dingle and Drake 2007, Hebblewhite and Merrill 2009). To assess how forage availability and security varied with migratory strategy, we delineated the landscape-scale geographic ranges used by migrants and residents, which represented habitat available for 2nd order selection. Within each study area, some deer migrated westward and some migrated eastward, thus, eastern versus western migrants were exposed to disparate resource availability. We delineated landscape-scale summer ranges separately for resident groups, eastward migrant groups, and westward migrant groups in each study area (Figure 2.1). For each group, we constructed a 100% minimum convex polygon (MCP) surrounding their GPS points. We added a 2 km buffer to each MCP to ensure they fully encapsulated individual home ranges to represent the areas collectively used by migrant and resident groups as summer range.

Quantifying summer nutritional resources — To quantify forage quality on the landscape, we used ground-based vegetation sampling and generalized linear models for estimating kcal of mule deer forage per m^2 across each of our study areas. To determine mule deer summer forage plants, we collected fecal pellet samples in each study area, then submitted samples to Jonah Ventures Laboratory (Boulder, CO, USA) for DNA metabarcoding to identify forage taxa. We only collected pellets from either mule deer we observed defecating, that were found fresh within 100m of mule deer we observed in the past 30 minutes, or that were located within 500 m of a cluster of GPS collar locations that uploaded within the last week. Samples were collected between June 1 and Aug. 31, 2017-2019, and consisted of 5-10 pellets collected from a single pellet group. Sampling effort was distributed across the full spatial extent of each study area. In

total, we submitted 160 samples: 53 from Cabinet-Salish, 64 from Rocky Mountain Front, and 43 from the Whitefish Range.

Through DNA metabarcoding analysis, forage plant taxonomy and the proportion of each taxa in individual deer diets were determined by analyzing exact sequence variants (ESV), which are nucleotide sequences that can differentiate species at a high resolution (Callahan et al. 2017). We aggregated DNA metabarcoding results by study area. Then, for each study area, we estimated how deer selected forage plants relative to their availability on the landscape by dividing the proportion of each forage plant in deer diets by the proportion of total forage biomass each forage plant made up on the landscape (our method for estimating species-specific biomass on the landscape is outlined below). Plants that made up at least 2% of deer diets in each study area, or that were consumed in greater proportion than their availability on the landscape, were considered "top forage plants" that mule deer consumed during summer. This resulted in 27 forage plants in Cabinet-Salish, 22 on the Rocky Mountain Front, and 24 in the Whitefish Range (Table A1).

We estimated phenological stage-specific digestible energy (DE, in kcal/g) of forage plants by collecting plants in different phenological stages (emergent, flowering, fruiting, mature seed, and senesced) during summer and submitting them to DairyOne Laboratories (Ithaca, NY) and the Wildlife Habitat Nutrition Laboratory (Pullman, Washington, USA) for sequential fiber analysis (Van Soest 1982). We then calculated the average DE across phenological stages for each plant to represent mean summer DE. We were unable to collect some forage plants in the field, because we had not determined all mule deer forage plants before our field work ended. For these missing plants, we used DE values reported in previous studies (Appendix A, TableA2; Hull 2018, Proffitt et al. 2016, Wagoner 2011). To estimate the abundance and distribution of

forage plants on the landscape, we conducted vegetation surveys across each study area to estimate species-specific forage biomass. Between summers 2017 – 2019, we surveyed 884 sites across 7 vegetation cover types (conifer forest, grasslands, deciduous shrublands, timber harvests, thins, prescribed fires, and burns) throughout our 3 study areas (Table A3). Sites were selected based on a stratified optimal allocation sampling design (Krebs 1999), and sample sizes were determined via power analysis (Appendix A). At each sampling site, we established a 40m transect along the contour of the hillslope. At the 0, 20, and 40m mark on the transect, we recorded plant species composition and visually estimated percent cover of vascular plant species within a $1m^2$ quadrat. In the corner of each $1m^2$ quadrat, we established a $0.5m^2$ clip plot in which we visually estimated percent cover of graminoids, forbs, and shrubs, then clipped and collected all of the aboveground biomass of these lifeforms within the clip plot into separate bags. Plant clippings were oven-dried at 50°C in a drying oven for 24 hours, and dry weight was measured to the nearest hundredth of a gram. Using the estimates of percent cover for each lifeform and their associated dry weight, we developed algorithms for estimating species-specific plant biomass based on percent cover and environmental site characteristics (Appendix A, Table A4). We applied these algorithms to estimate species-specific biomass (in g/m^2) of forage plants at each site. We then combined our forage DE data with species-specific biomass estimates to calculate the kcal of forage plants per m^2 at each sampling site. We developed generalized linear models with remotely-sensed covariates for predicting mean forage quality ($kcal/m^2$) during summer across each of our study areas (Appendix A, Table A6). Because of the geographic proximity and similar climatic conditions of the Cabinet-Salish and Whitefish Range, we combined data from those study areas to develop a single forage quality model there. Forage quality was modeled separately for the Rocky Mountain Front.

Estimating wolf and mountain lion predation risk — To estimate predation risk from wolves and mountain lions, we used previously developed wolf and mountain lion RSFs that estimated the probability of encountering those predators during summer (see Chapter 1). Wolf RSFs were developed using GPS collar data from 13 packs and 18 individual wolves across our 3 study areas, and separate RSFs were developed for each study area. Mountain lion RSFs were developed using GPS collar data from 17 mountain lions in the Garnet Range of west central Montana. We extrapolated Garnet mountain lion RSFs to our study areas and tested their predictive performance on Very High Frequency (VHF) collar data from mountain lions in the Whitefish Range and the Rocky Mountain Front. To improve predictive performance, the mountain lion RSF developed for the Rocky Mountain Front contained different covariates than the RSF used in the Cabinet-Salish and Whitefish Range (Chapter 1). To standardize predator RSF values for comparison across study areas, we converted predicted values to the percentile scale, where 0 represented the lowest predicted RSF value and 100 represented the highest predicted value (Kohl et al. 2019).

Forage-security correlation — To determine whether mule deer faced a tradeoff between forage and security from predators, we used GIS programming in R to measure predicted forage quality and wolf and mountain lion RSF values from 1,000 random points within each study area. We calculated the Pearson's correlation coefficient (r) between forage quality and security within each study area and visually assessed correlations between forage and security.

Testing for differences in resource availability between migrants and residents — We used linear regression to test for differences in average forage quality between migrant and resident population-level summer ranges within each study area. Our sample units were individual vegetation sampling locations, and we modeled forage quality ($kcal/m^2$) at each vegetation

sampling location as a function of study area, migrant or resident summer range, and an interaction between study area and migratory strategy. We log-transformed the response variable to satisfy assumptions of normality. Vegetation sampling was unbalanced among different vegetation cover-types within each study area, so when comparing mean forage quality between summer ranges, we avoided over-representing vegetation cover-types that took up little geographic space but were heavily sampled. To do this, each sample was weighted by $w_{i_{CS}} = \frac{A_{CS}}{P_{CS}}$, where each sample *i* was assigned weight *w* equal to *A* (the proportion of area in study area *S* consisting of cover-type *C*) divided by *P* (the proportion of samples in study area *S* falling in cover-type *C*). To test for differences in average predation risk between migrant and resident summer ranges, we used the 'raster' package (Hijmans 2018) in R to randomly sample 100 points within each range and measured predicted values of wolf and mountain lion predation risk (on the percentile scale) at these points. We used the same linear regression framework to test for differences in wolf and mountain lion predation risk as we did for assessing forage quality, but did not weight samples because they were sampled randomly across vegetation cover-types.

Resource selection analyses

To address how resource selection varied between migratory strategies and across different levels of forage availability, we developed 2nd order (home range scale) and 3rd order (within-home range scale) summer RSFs for mule deer. For every individual, we estimated year-specific summer home ranges using a 90% kernel density estimate (KDEs) with smoothing parameter h = 0.01 (Kie et al. 2010). We used 90% KDEs because we felt 95% KDEs were excessively large and did not represent the areas where mule deer conducted foraging and fawn-rearing activities on a daily basis (Burt 1943). For every individual, we combined year-specific summer home

ranges across years to create a single, multi-year summer home range per deer (Hebblewhite and Merrill 2009). At the 2nd order, we defined used locations as random points from within individual home ranges equal to the number of GPS points uploaded per individual (Decesare et al. 2012). We considered each population-level range of migrants and residents to be available for home range selection by individuals of that migratory strategy in each study area. We sampled available points within population-level ranges randomly, equal to 5 times the number of GPS points within each population-level range (DeCesare et al. 2012). At the 3rd order we defined used points as the GPS points that uploaded for each individual within their home range. We sampled available points within individual home ranges randomly equal to the number of GPS points uploaded per individual. Thus, used points at the home range scale were available points at the within-home range scale (DeCesare et al. 2012).

We used hierarchical mixed-effects RSFs in a Bayesian framework to model summer habitat selection by mule deer (Manly et al. 2002; Thomas et al. 2006). This framework simultaneously estimated selection coefficients for covariates at the individual-level, migratory strategy-level, and population level, and also accounted for unbalanced samples of used locations between individuals (Thomas et al. 2006). The model consisted of four parts: a data (likelihood) model, an individual parameter model, and 2 hyperparameter models (for migratory strategy-level and population-level parameters, respectively). At each spatial scale, our likelihood model took the form of a logistic regression, which estimated individual relative probabilities of selection for resource covariates using the logit-link function:

$$logit(p_j) = \left(\beta_0 + \beta_{1_i}\text{Forage}_{j,i} + \beta_{2_i}\text{Wolf}_{j,i} + \beta_{3_i}\text{Mountain lion}_{j,i} + \gamma_{0_i}\right)$$

Where observations $j = 1\ldots n$ are clustered within individuals $i = 1\ldots m$, β_0 is the mean intercept, $\beta_{1\ldots3}$ are random slope coefficients for forage quality, wolf predation risk, and mountain lion

predation risk covariates for every individual *i*, and γ_{0_i} are random intercepts for individuals (Gillies et al. 2006). Within our model framework, individual selection coefficients (e.g. β_{x_i} , the slope coefficient of covariate *x* for individual *i*) were treated as random effects with individual prior distributions informed by the prior distributions (hyperpriors) of migratory strategy-level coefficients (hyperparameters; Thomas et al. 2006). For example, the coefficient for the effect of forage on selection by individual *i* was modeled as a normal random variable, $\beta_{Forage_i} \sim N\left(\mu_{Forage_s}, \sigma_{Forage}\right)$, where μ_{Forage_s} represented the mean effect of forage on selection by deer with migratory strategy *s*. We assumed migratory strategy-level coefficients followed a similar normal distribution with a mean equal to the population-level mean effect of covariate *x*. Hyperparameters were modeled with uninformed prior distributions for means (e.g. $[\mu_{Forage_s} \sim N(\mu = 1, \sigma = 1000)]$) and variances (e.g. $[\sigma^2_{Forage} \sim Inverse\ Gamma\ (1,1)]$).

Of the GPS collars deployed on deer included in RSF analyses, upload rates to Globalstar satellites (hereafter fix rates) ranged from 29.98% to 100% ($\bar{x}$ = 72%; Appendix B, Table B1). Lower fix rates of some collars may have been a result of habitat-induced biases, which can affect RSF modeling (Frair et al. 2010). We corrected for these biases by developing a spatial model to predict the probability of a collar acquiring a fix (*Pfix*) as a function of topography and tree canopy cover, which commonly affect GPS collar fix rates (Frair et al. 2010). Our *Pfix* model was developed using store-on-board collar data from 9 GPS collars recovered from mule deer that had died across our 3 study areas (see Appendix B for detailed methods and results on *Pfix* modeling). We accounted for habitat-induced GPS collar fix bias in our 3rd order RSFs by weighting used locations by 1/*Pfix*. We implemented this weighting by assuming the likelihood of location *j* being used was Bernoulli distributed as:

$$P(use)_j \sim bern(logit(p_j) \times Pfix_j)$$

We estimated marginal distributions for posterior likelihoods of model parameters using JAGS 4.3.0 (Plummer 2003), which we implemented via the "rjags" package (Plummer 2018) in program R. We ran each model for 5000 iterations in 3 parallel chains with a 1000 iteration burn-in period and retained every 2nd sample for a total of 7500 samples per model. We assessed model convergence by inspecting $\hat{R}$ values for good convergence ($\hat{R} \leq 1.1$; Gelman et al. 2014) and by visually inspecting trace plots and posterior distributions for each parameter. We derived study area and group-level parameters (where 3 study areas × 2 migratory strategies defined 6 groups) by averaging individual-level parameters for a given study area or group outside of our JAGS models. Thus, error for study-area and group-level parameters was computed based on variance in the means of individual-level parameters, rather than error associated with the effect of environmental covariates (Sawyer et al. 2006, Thurfjell et al. 2014), and is reported as frequentist confidence intervals rather than Bayesian credible intervals (Figure 2.3B; 2.4 A).

At each spatial scale, we tested RSFs that included forage quality, mountain lion predation risk, and wolf predation risk as covariates. Continuous covariates were centered on their mean and scaled by standard deviation units. We used linear regression to determine how forage availability influenced the selection coefficients estimated by the RSFs using:

$$\beta_{x_s} = \theta_{0_s} + \theta_{1_s}(\log(\overline{m}_s^A(forage))$$

Where β_{x_s} is a vector of group or individual-level selection coefficients for resource *x* (forage, wolf, or mountain lion risk) at scale *s* (2nd order or 3rd order, respectively), $\overline{m}_s^A(forage)$ is a vector of mean values of forage quality at available units at scale *s*, θ_{0_s} is the y intercept, and θ_{1_s} is the slope for the effect of forage availability on selection coefficients at each scale (Holbrook

et al. 2019). At the 2nd order, β_{x_2} represented group-level selection coefficients for forage, wolf risk, and mountain lion risk and $\bar{m}_3^A(forage)$ represented mean forage quality across 2nd order available points. At the 3rd order, β_{x_3} represented individual-level selection coefficients and $\bar{m}_3^A(forage)$ represented mean forage quality within individual home ranges. We visualized these relationships by plotting selection coefficients against forage availability at each scale.

RESULTS

Classifying deer into migratory strategies

We classified migratory strategies of 110 mule deer. Overall, 80% were migrants (n = 88) and 20% were residents (n = 22). The Whitefish Range had the highest proportion of migrants (84%) and the Rocky Mountain Front had the lowest (77%; Appendix C, Table C1). A single disperser on the Rocky Mountain Front travelled 31.49 km from its winter home range to a new home range in spring of 2017, and never left this home range by the time monitoring ended in Fall 2019; we re-classified this deer as a resident. On the Rocky Mountain Front, mule deer over-wintered in the eastern prairie portion of this study area. Migrants primarily traveled westward and spent their summers in the mountains of the Bob Marshall, though a small portion migrated further eastward into the prairie for summer. Residents remained within the prairie all summer-long (Figure 2.1). In the Cabinet-Salish, mule deer over-wintered in the Fisher River drainage. Migrants either traveled westward into the Cabinets or eastward into the Salish Range. Residents generally remained within the Fisher drainage all summer-long (Figure 2.1). In the Whitefish Range, mule deer over-wintered on the western base of the mountains. Migrants generally traveled east into the Whitefish Range, sometimes passing the crest of the mountains to summer in the watershed of the North Fork of the Flathead River or crossing the border into British

Columbia, Canada. Residents remained at the western base of the mountains summer-long (Figure 2.1).

Comparing forage and risk in migrant and resident ranges

We found little differences in forage quality between migrants and resident summer ranges in the Rocky Mountain Front Whitefish Range (Table 2.1). In Cabinet-Salish, average forage quality was 1.43 kcal/m^2 higher in resident summer range than in migrant summer range (P = 0.071; Table 2.1). On the Rocky Mountain Front, wolf predation risk was 19% higher for residents than for migrants (P < 0.001), and mountain lion predation risk was 27% lower (P < 0.001), but there were little differences in predation risk between migrants and residents in other study areas (Table 2.1). In Cabinet-Salish and Whitefish, forage quality and wolf predation risk had slight positive correlations (r = 0.112 and 0.129, respectively), but were negatively correlated on the Rocky Mountain Front (r = -0.346; Figure 2.2). In Cabinet-Salish, Whitefish, and on the Rocky Mountain Front, forage quality and mountain lion predation risk were positively correlated (r = 0.11, 0.018, and 0.335, respectively; Figure 2.2).

Resource selection analyses

Selection coefficients for forage quality, wolf predation risk, and mountain lion predation risk converged at the migratory strategy and individual-level in our 2nd and 3rd order RSFs ($\hat{R} \leq 1.1$). Neither migrants or residents selected for forage quality at the 2nd order. For both migrants and residents, the odds of selection for forage at the 2nd order were 1.01 times lower for every 1 unit increase in kcal/m^2 (Table 2.2; Figure 2.3B). Migrants and residents avoided mountain lions and were neutral (mean selection coefficients were near zero) towards wolves at the 2nd order (Table 2.2; Figure 2.3B). At the 3rd order, migrants and residents both selected for forage quality and

avoided wolf and mountain lion predation risk, despite positive forage-mountain lion risk correlations. A migrant's odds of selection for forage quality at the 3rd order were 1.142 times greater for every 1 unit increase in kcal/m^2, whereas a resident's odds of selection were 1.152 times greater (Table 2.2; Figure 2.3B).

2nd order selection for forage or security by groups did not vary as a function of available forage in landscape-scale summer ranges, and stronger selection for forage at the 2nd order did not correspond with weaker avoidance of predation risk (Figure 2.4A). 3rd order selection for forage by individuals decreased as forage availability in individual home ranges increased. For every 1 kcal/m^2 increase in mean forage quality within individual home ranges, odds of selection for forage decreased by 0.596 (P = 0.002; Figure 2.4B). We found marginal evidence that as forage availability within individual home ranges increased, individuals showed weaker 3rd order avoidance of mountain lions (Figure 2.4B). Odds of selection for areas with higher mountain lion predation risk increased by 0.71 (P = 0.09) for every 1 kcal/m^2 increase in mean forage quality within individual home ranges (Figure 2.4B). 3rd order avoidance of wolf predation risk did not vary as a function of forage availability in home ranges.

DISCUSSION

Across all study areas, the availability of forage quality did not differ substantially between migrant and resident summer ranges, and predation risk did not differ predictably. Selection for forage and avoidance of risk across migratory strategies and ecosystem-types by mule deer was highly consistent. Specifically, migrants and residents both avoided mountain lions at the 2nd order, but did not select forage or avoid wolves at that scale. At the 3rd order, migrants and residents both selected for forage and avoided mountain lions and wolves. We found mixed

support for our hypothesis that as forage availability increased at a given spatial scale, mule deer would be free to forego selection of forage and strongly avoid predation risk at a subsequently finer scale. At the 2nd order, selection for forage and avoidance of risk occurred independently of forage availability within migrant and resident summer ranges. Forage quality and mountain lion predation risk were positively correlated (Figure 2.2), so we expected individuals exhibiting weak selection for forage would more strongly avoid mountain lions. However, at the 3rd order, individuals with higher forage quality within their home ranges showed weaker selection for forage quality and weaker avoidance of mountain lions (Figure 2.4B). This suggests that positive correlations between forage and mountain lion predation risk were decoupled as mule deer selected habitat at fine spatial scales.

Counter to common findings (Fryxell and Sinclair 1988, Albon and Langvatn 1992, Hebblewhite and Merrill 2009), we detected a high degree of similarity in forage conditions between migrant and resident summer ranges. Further, risk from predators did not differ predictably between migrants and residents. Both groups selected for forage and avoided predators similarly at finer scales, lending some support to the *resource parity* hypothesis. Regardless of these similarities, the proportion of migrants was at least 3.5 times greater than the proportion of residents in every study area, suggesting some benefit was associated with migrant strategies. There are multiple reasons why migrating could be beneficial, beyond immediate forage benefits. In the past, summer range conditions may have favored migratory mule deer, but recent changes in habitat may have reduced the forage benefits of migration. For example, forest disturbances that can improve forage conditions for mule deer, like low to moderate severity wildfires and timber harvests (Hayes 2020, in prep; Proffitt et al. 2016; Hayden et al. 2008), have decreased in frequency in the mountains of Western Montana over the past half century

(Stephens et al. 2009, McIver et al. 2013, Halofsky et al. 2020), which could account for reduced forage quality in migratory mule deer ranges. Alternatively, migration may expose mule deer to higher summer forage quality on average over time, but stochastic events like wildfires or droughts could lead to fluctuations in the relative forage benefits of migrant versus resident strategies in a given year (Proffitt et al. 2016; Middleton et al. 2013). The benefits of each strategy may balance out over longer time scales than our 3-year study, allowing partial migration to persist (Schindler et al. 2010).

It is important to note that our method for estimating forage quality may have over-represented the contribution of certain plants, like graminoids, towards available forage quality for mule deer. We considered any plant taxa that composed ≥2% of mule deer diets by study area to be a forage plant, resulting in graminoids like *Bromus spp.* contributing towards estimates of kcal/m^2 (Appendix A, Table A1). As concentrate selectors, mule deer are incapable of consuming high volumes of low-quality food like mature grasses (Baker and Hansen 1985, Hofmann 1989), and require a mixed diet of forbs, shrubs, and graminoids to meet their nutritional needs (Hobbs and Swift 1985). Therefore, when a single forage species is highly abundant on the landscape, only a fraction of its digestible energy may be truly usable for mule deer. For example, in the summer range of residents on the Rocky Mountain Front (located primarily in shortgrass prairie), graminoids contributed towards 51% of forage biomass on the landscape, but composed only 9% of mule deer diets in that study area (Appendix A, Figure A1). Thus, we may have over-estimated the availability of forage for residents relative to migrants, which could account for the higher proportion of migrants than residents we observed in each study area.

Selection for forage and security across migratory strategies and ecosystem-types by mule deer was highly consistent. These similarities in behaviors of mule deer may have arisen due to a shared strategy for avoiding their most lethal predator when selecting home ranges, and for maximizing forage within home ranges. In selecting home ranges, mule deer generally did not select for forage quality, and selection for forage was unaffected by its availability in summer range, potentially because they can't perceive forage availability at such a broad scale (Battin 2004). Due to changes in vegetation communities and stochastic climate patterns, the spatial distribution of forage quality is unpredictable on an annual basis (Middleton et al. 2013, Hurley et al. 2014), which may make it difficult for mule deer to select high forage quality home ranges annually. Rather, home range placement may be driven by predation risk, which may vary less in space between years. Mountain lion habitat preferences are driven largely by hiding cover and stationary topographic features (Blake and Gese 2016; see Chapter 1), which mule deer may more easily perceive at broad scales and predict annually, enabling them to select low risk home ranges. Wolves were not avoided when selecting home ranges, perhaps due to the lower lethality of wolves versus mountain lions we documented. Out of 26 predator-caused mule deer mortalities in our study, 21 were caused by mountain lions, 4 by wolves, and 1 by coyotes. The influence of the apparently more lethal predator (mountain lions) on home range selection may have overridden the influence of the less lethal predator (wolves), which is a common behavioral response of prey in multi-predator systems (Relyea 2003, Morosinotto et al. 2010, Kohl et al. 2019).

There are other potential mechanisms for partial migration's persistence in our study system that we cannot eliminate, including migration as a tradeoff between forage and security. Migratory mule deer often receive nutritional benefits by tracking the "green-wave" of emerging

forage (Lendrum et al. 2014, Aikens et al. 2017). We were unable to predict temporal changes in plant phenology in our forage quality models as others have (Hebblewhite et al. 2008, Proffitt et al. 2016), though observed little variation in phenological stage-specific DE of forage plants (Appendix A, Table A2; (Wagoner 2011, Proffitt et al. 2016, Hull 2018). Nevertheless, the nutritional benefits of delayed plant phenology for migrants can improve mule deer survival (Hurley et al. 2014), so migrants may have received forage benefits we were unable to account for. Our estimates of predation risk assumed predator densities were equal within migrant and resident ranges, which could be a false assumption for mountain lions (Robinson et al. 2015) and wolves (Sells 2019) in our study system, so predation risk may have been less similar between migrant and resident ranges than we documented. However, statewide models predict a high probability of wolf occupancy throughout all our study areas (Montana Fish Wildlife and Parks 2018*a*) and estimated mountain lion densities in Western Montana are among the highest in North America (Russell et al. 2012, Robinson et al. 2014, Proffitt et al. 2015), so we think it's a fair assumption that wolf and mountain lion densities were relatively high throughout all of our study areas.

MANAGEMENT IMPLICATIONS

Given their low plasticity in summer home range selection, and the importance of selecting high quality forage within-home ranges, habitat treatments that improve forage quality and reduce predation risk from mountain lions within summer home ranges may be an effective means of improving mule deer habitat. This could be especially effective in declining populations with a high proportion of migrants. Wildlife managers in Western Montana could use our 2nd order RSFs to identify where mule deer home ranges are likely to be, which could indicate where habitat treatments should take place. Treatments like timber harvests, thins, and wildfires may

improve forage quality and reduce hiding cover used by mountain lions within summer home ranges of mule deer (Hayes 2020, in prep; Appendix A, Table A6, Figure A2).

Table 2.1 Means and standard errors (SE) of forage quality, wolf predation risk, and mountain lion predation risk within migrant and resident summer ranges by study area. Mean values of forage quality were estimated by calculating average forage quality within each vegetation cover-type, weighting these averages by the proportion area each cover-type composed within each summer range, then averaging those weighted means. 'Res. - Mig.' represents results from weighted linear regression for forage, and unweighted linear regression for predation risk, testing for differences between each variable in resident and migrant summer ranges by study area, and P values were derived in that linear regression.

Variable	Study Area	Strategy	Mean	SE	Res. - Mig.	P
Forage quality (Kcal/m2)	Cabinet-Salish	Mig.	0.99	0.31	1.43	0.071
		Res.	1.29	0.50		
	Rocky Mtn. Front	Mig.	1.49	0.92	0.91	0.673
		Res.	2.70	1.28		
	Whitefish	Mig.	1.28	0.63	1.33	0.192
		Res.	1.37	0.73		
Wolf risk (percentiles)	Cabinet-Salish	Mig.	54.90	2.63	-3.64	0.365
		Res.	51.30	3.03		
	Rocky Mtn. Front	Mig.	38.90	2.91	19.01	<0.001
		Res.	57.90	2.74		
	Whitefish	Mig.	50.80	3.07	1.36	0.735
		Res.	52.20	2.64		
Mountain lion (percentiles)	Cabinet-Salish	Mig.	57.10	2.98	5.01	0.195
		Res.	52.10	2.90		
	Rocky Mtn. Front	Mig.	64.70	2.61	-26.79	<0.001
		Res.	37.90	2.34		
	Whitefish	Mig.	50.30	2.81	3.18	0.41
		Res.	53.40	2.69		

Table 2.2 Posterior means, standard deviations, and credible intervals (CI) of migratory strategy-level slope coefficients (centered and scaled) derived from 2nd and 3rd order hierarchical Bayesian RSFs.

Scale	Strategy	Variable	Mean	SD	CI		Rhat
					2.50%	97.50%	
2nd order	migrant	forage	-0.040	0.197	-0.435	0.346	1
		lion	-0.445	0.164	-0.767	-0.124	1
		wolf	0.025	0.046	-0.065	0.115	1
	resident	forage	-0.051	0.345	-0.742	0.624	1
		lion	-1.204	0.317	-1.837	-0.592	1
		wolf	-0.029	0.088	-0.200	0.142	1
3rd order	migrant	forage	0.534	0.159	0.221	0.845	1
		lion	-1.124	0.338	-1.788	-0.462	1.02
		wolf	-0.655	0.088	-0.828	-0.483	1
	resident	forage	0.570	0.298	-0.010	1.163	1
		lion	-1.352	0.595	-2.577	-0.216	1.02
		wolf	-0.751	0.169	-1.083	-0.419	1

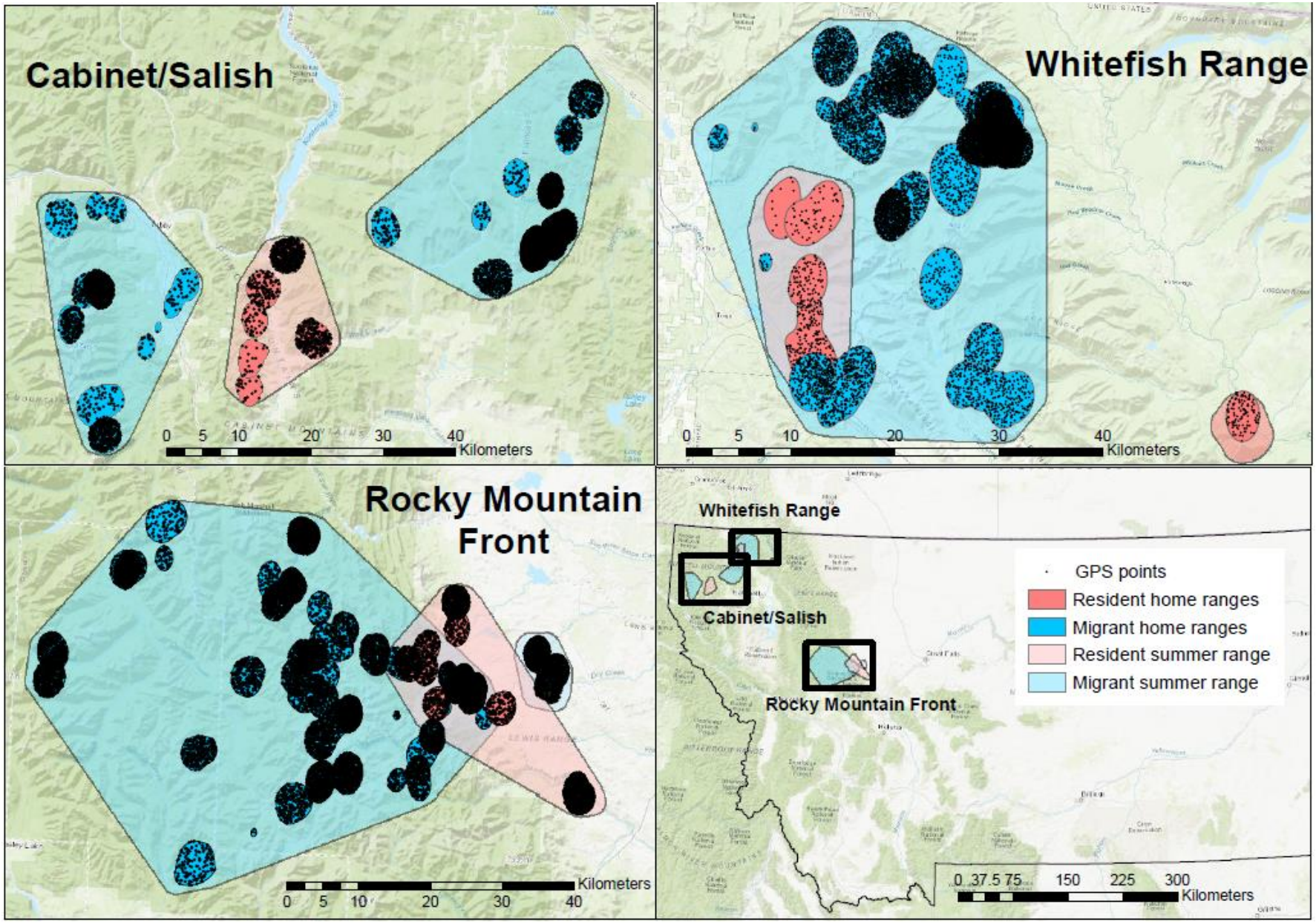

Figure 2.1. Study areas for mule deer habitat selection analyses throughout western Montana. Landscape-scale summer ranges for migrants and residents available for home range selection were determined by creating a specific MCP (large polygons) around summer locations of deer in every study area by migratory strategy, estimated separately for eastward and westward migrants. Multi-year summer home ranges of individuals were estimated using 90% KDEs (smaller polygons). Summer GPS points of deer are plotted as well.

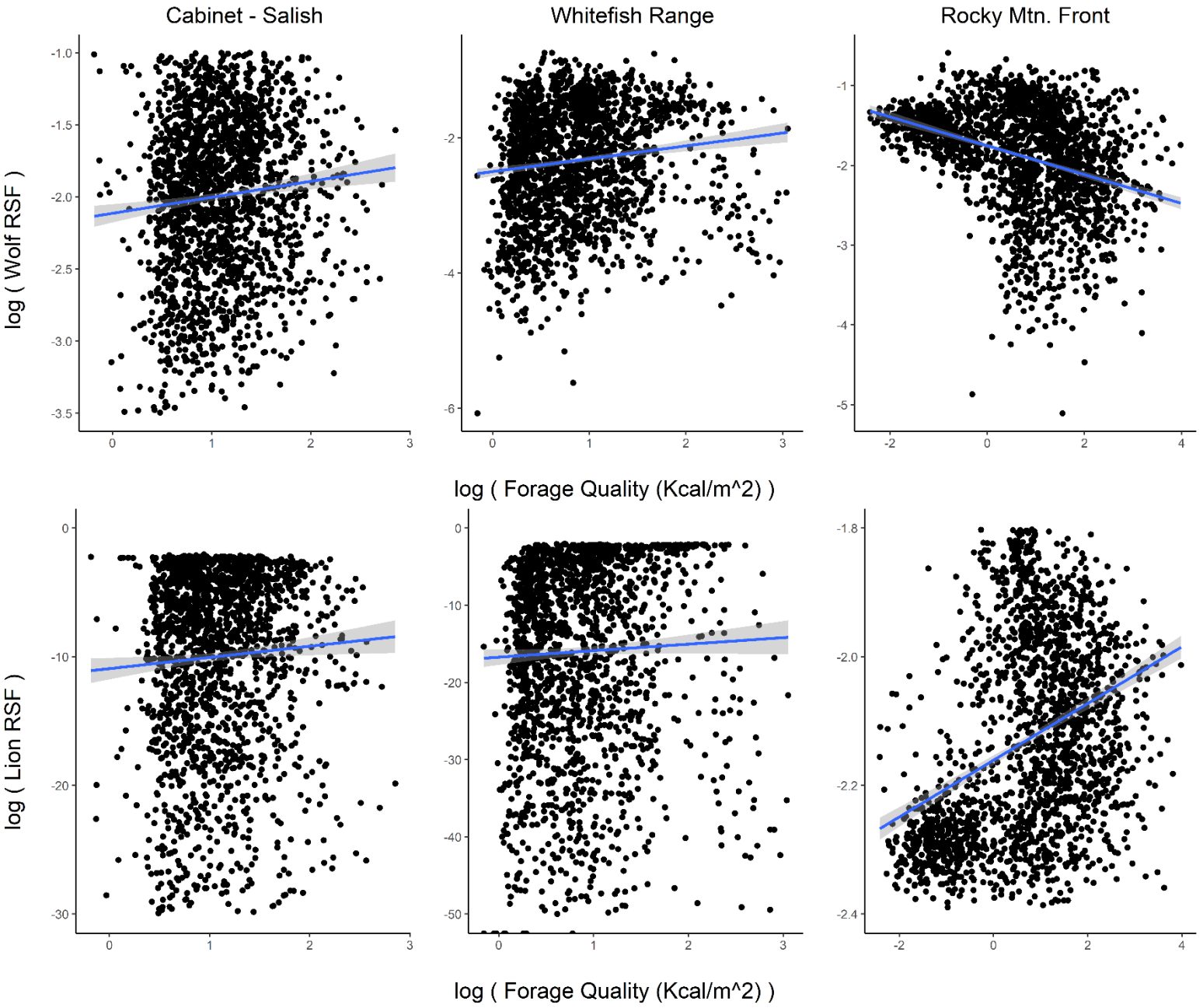

Figure 2.2 Relationships between predicted forage quality and predation risk from wolves and mountain lions in 3 study areas in Western Montana. Relationships were assessed by randomly sampling 1000 points per migrant and resident summer range per study area (n = 2000 points per study area). Predicted forage quality and predator RSF values were log-transformed to normalize their distributions so linear relations could be assessed.

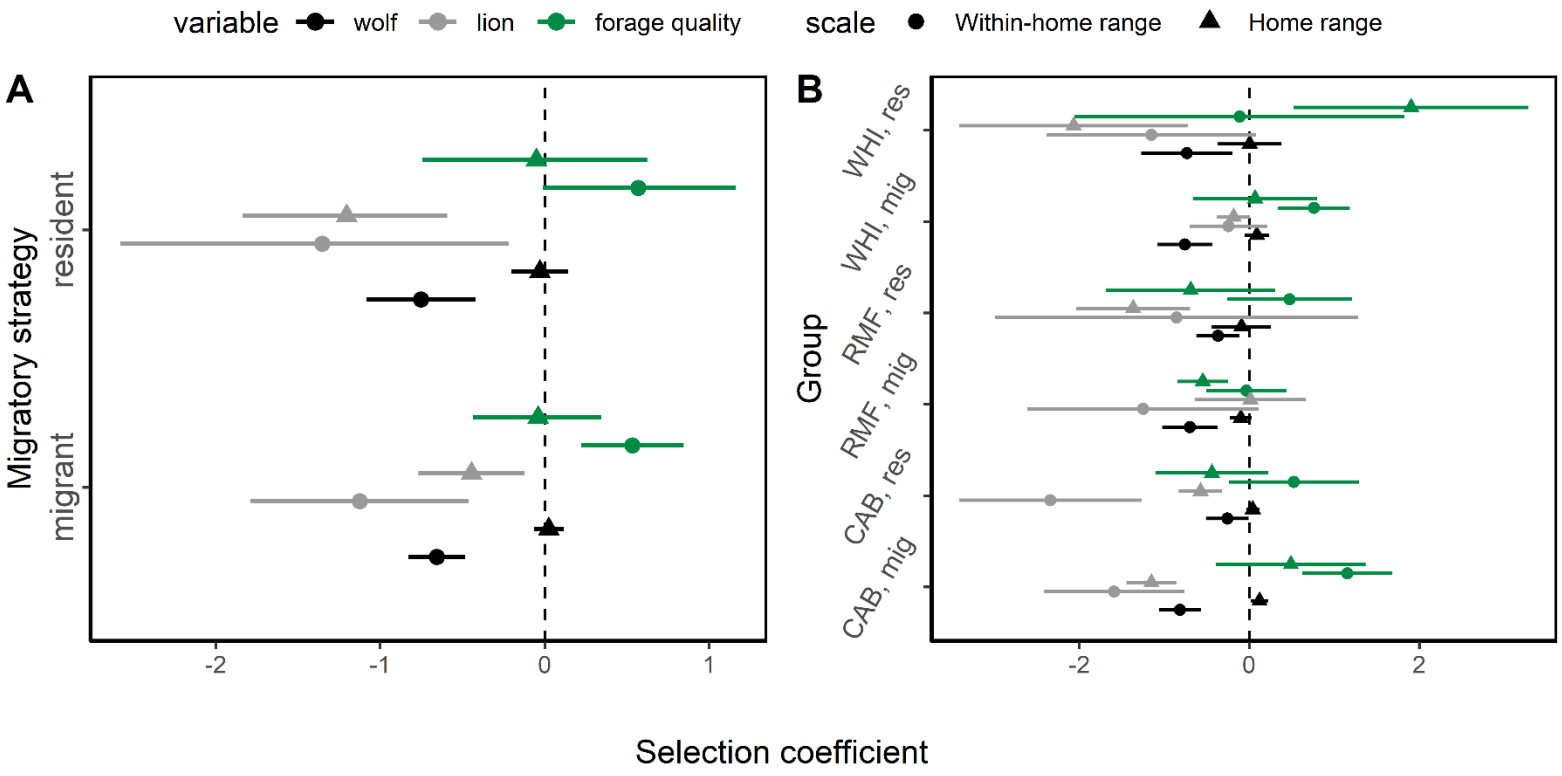

Figure 2.3 Centered and scaled selection coefficients from Bayesian hierarchical RSFs. Parameters were computed at multiple grouping levels including (**A**) specific migratory strategies and (**B**) groups of mule deer in each study area by migratory strategy. Y-axis labels in plot B refer to study area and migratory strategy ('CAB': Cabinet-Salish, 'RMF': Rocky Mtn. Front, 'WHI': Whitefish, 'mig': migrant, 'res': residents). Error bars in plot B represent 95% confidence intervals, not credible intervals, because group-level coefficients were calculated by averaging individual-level coefficients outside of our Bayesian model.

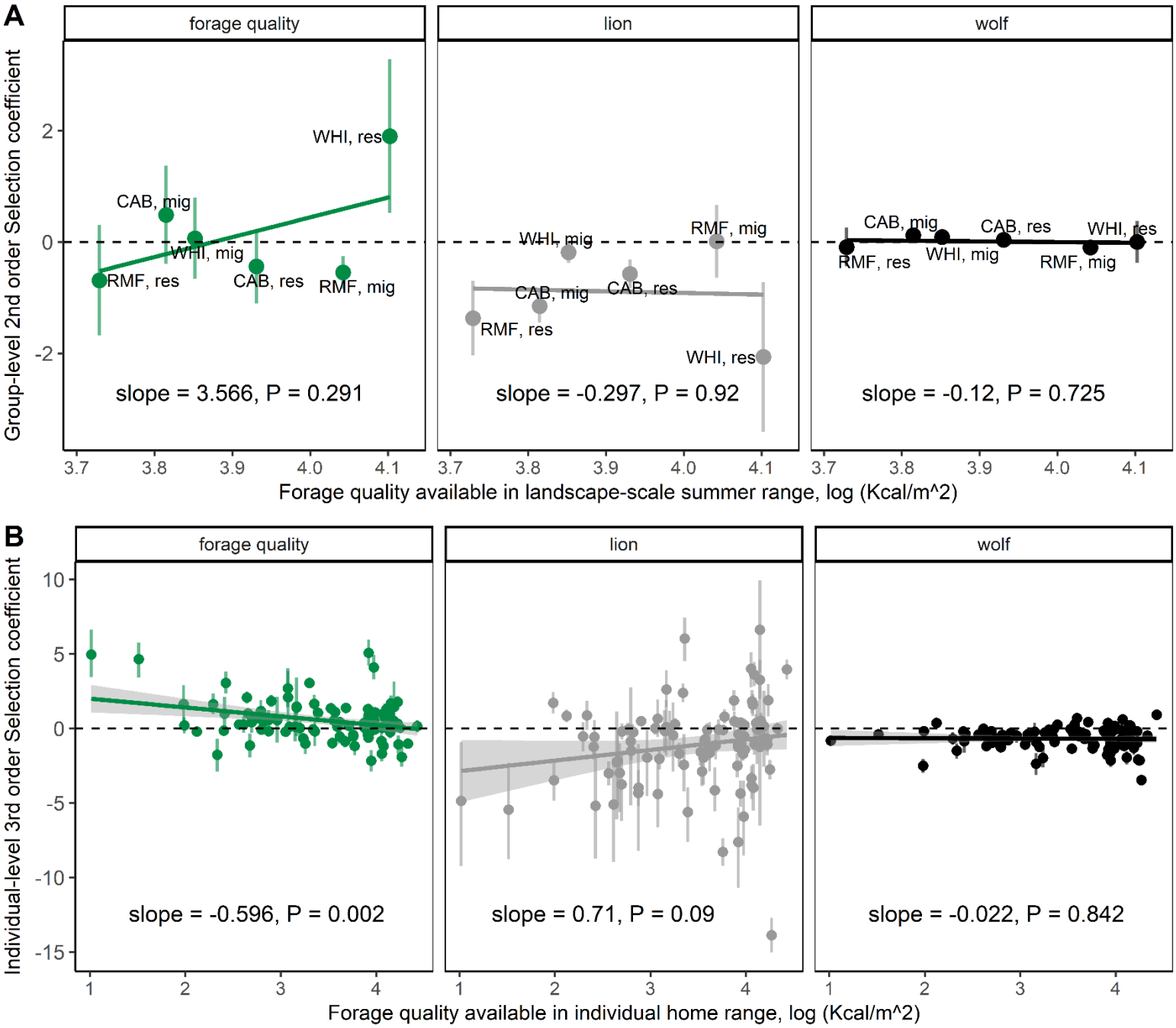

Figure 2.4 (**A**) Centered and scaled group-level selection coefficients from 2nd order RSFs plotted against mean forage quality (log-transformed) available in landscape-scale migrant or resident summer ranges, labeled by group ('CAB': Cabinet-Salish, 'RMF': Rocky Mtn. Front, 'WHI': Whitefish, 'mig': migrant, 'res': residents). Error bars represent 95% confidence intervals, not credible intervals, because group-level coefficients were calculated by averaging individual-level coefficients outside of our Bayesian model. (**B**) Individual-level coefficients and 95% credible intervals from 3rd order RSFs plotted against forage availability in individual home ranges.

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Appendix A.

Estimating diet composition and quality of forage plants for mule deer, and developing landscape nutrition models

Determining summer forage plants

To determine mule deer summer forage plants, we collected pellet samples in each study area, then submitted samples to Jonah Ventures Laboratory (Boulder, CO, USA) for DNA metabarcoding to identify forage taxa. Since mule deer and white-tailed deer pellets are visually indistinguishable, we only collected pellets from either mule deer we observed defecating, that were found fresh within 100m of mule deer we observed in the past 30 minutes, or that were located within 500 m of clusters of GPS collar locations that uploaded within the last week. We primarily collected moist, fresh pellets, but when we were unable to find moist pellets, we collected dry, dark pellets with a pliable consistency and strong odor. A sample consisted of 5-10 pellets collected from a single pellet group. Samples were collected between June 1 and Aug. 31, 2017-2019. Sampling effort was distributed across the full spatial extent of each study area. In total, we submitted 160 samples: 53 from Cabinet-Salish, 64 from Rocky Mountain Front, and 43 from the Whitefish Range.

Through DNA metabarcoding analysis, forage plants were identified to the finest taxonomic resolution possible by analyzing exact sequence variants (ESV), which are nucleotide sequences that can differentiate species at a high resolution (Callahan et al. 2017). DNA metabarcoding results provided both plant species present in mule deer diets, and estimates of the relative proportion of those species in individual deer diets. We aggregated DNA metabarcoding results by study area, and determined the proportion of each species in collective diet of deer in each study area. Our DNA metabarcoding results returned many plant species that were not present in Montana, but were congeneric with plants we observed in the field. We assumed this was due to misidentification of true forage species that were missing from the ESV reference library used for identifying plants in the diet. For misidentified species we considered

their entire genus to be forage plants for mule deer. We then estimated how deer selected forage plants relative to their availability on the landscape by dividing the proportion of each forage plant in deer diets by the proportion of biomass of each forage plant by study area (our method for estimating species-specific biomass on the landscape is outlined below). Plants that made up at least 2% of deer diets in each study area, or that were used disproportionately to their availability on the landscape, were considered "top forage plants" that mule deer consumed during summer (June 1 – Aug 31). This resulted in 27 forage plants in Cabinet-Salish, 22 on the Rocky Mountain Front, and 24 in the Whitefish Range (Table A1).

Quality of mule deer forage plants

To evaluate quality of forage plants, we estimated their mean summer digestible energy across phenological stages (DE in kcal/g) using sequential detergent fiber analysis (Van Soest 1982) for a subset of forage plants collected in the field, and used DE values from previous studies for remaining plants. We had not yet determined deer diet composition while we were conducting field work, thus we were unable to collect samples of all forage plants for quality analysis. We collected plants we suspected were mule deer forage species based on field observations. Of those plants, we collected multiple samples from each phenological stage present between June 1 and Aug. 1 (i.e. emergent, flowering, fruiting, mature seed, or senescent stages). For forage plants we collected, we calculated the mean phenological stage-specific percent dry matter digestibility (DMD) using the following equation from Robbins et al. (1987a, b):

Equation 1. $$DMD = [(0.9231\ e^{-0.0451*ADF} - 0.03*AIA)\ (NDF)] + [(-16.03 + 1.02\ NDS) - 2.8*P]$$

where ADL is acid detergent lignin (%), AIA is acid insoluble ash (%) of monocots, NDF is neutral detergent fiber (%), NDS is neutral detergent soluble (%), and P is the reduction in

protein digestion (%). P is estimated as 11.82*BSA, where BSA is the level of bovine serum albumin (Robbins et al. 1987b). BSA is an index of the inhibiting effect of increasing tannins measured in milligrams of BSA precipitated per milligram of dry matter forage. ADL, AIA, NDF, and NDS values were obtained from the Wildlife Habitat Nutrition Laboratory (Pullman, Washington, USA). BSA values for shrubs containing tannins were obtained from DairyOne laboratories (Ithaca, NY) and were assumed to be 0 for forbs and graminoids that typically do not contain tannins.

We then estimated phenological stage-specific digestible energy of each forage plant collected using an equation from Cook et al. (2016):

$$\text{Equation 2.} \qquad DE = (DMD/100) * GE$$

where GE is gross energy content estimated as 4.53 kcal/g for forbs, graminoids, and deciduous shrubs and 4.8 kcal/g for evergreen shrubs (Cook et al. 2016). We then averaged across phelonogical stage-specific DE values to estimate mean summer DE of forage plants. For forage plants that weren't collected in the field, we used DE values reported in previous studies conducted in either SW Montana (Proffitt et al. 2016), NE Washington (Hull 2018), or NE Oregon (Wagoner 2011; Table A2). There were some forage plants for which we were unable to obtain DE values, but the vast majority of these plants comprised <2% of deer diets by study area (Table A2).

Power analyses for determining vegetation sample size goals

To determine the number of transects we needed to survey to represent the variability of forage plant species distribution and biomass across vegetation cover-types, we conducted a power analysis before our initial field campaign. We used elk forage biomass data from the Ya-Ha

Tinda Ranch, AB, Canada (Hebblewhite et al. 2008) to conduct this analysis. Using the mean and SD of herbaceous biomass (forbs and graminoids) in different vegetation cover types reported by Hebblewhite et al., we simulated log-normal sampling distributions of herbaceous biomass for the vegetation cover types surveyed in our own study. We took random sub-samples from these distributions ranging from size n = 1 to n = 45. With each sub-sample of size n, we calculated the coefficient of variance (CV = standard error / mean) of herbaceous biomass. We replicated this procedure 500 times, and then determined the minimum number of samples to achieve CV = 0.10 (Krebs 1999; Table A3). After our first 2 field seasons (summer 2017 on the Rocky Mountain Front and summer 2018 in all 3 study areas), we conducted another power analysis using our own field data to determine remaining sample size goals. We estimated the mean and SD of herbaceous biomass within the 7 vegetation cover types we surveyed by bootstrapping for these parameters with our 2017-18 data. We used sampling distributions of herbaceous biomass measured at 190 sites in conifer forests, 34 sites in deciduous shrublands, 82 sites in grasslands, 41 sites in timber harvests, 27 sites in prescribed fires, 37 sites in thins, and 98 sites in burns. Based on these sampling distributions, we determined the minimum number of samples to achieve CV=0.10 within each vegetation cover type for each study area, and sought to achieve these sample sizes in our final field season in summer 2019 (Table A3). We sampled conifer forests beyond the minimum sample sizes needed, because conifer sites were being analyzed as part of a separate analysis comparing vegetation communities in disturbed versus undisturbed forests (Hayes 2020, in prep).

Field Methods for Estimating Forage Plant Biomass.

We measured plant species distribution and biomass by surveying vegetation in quadrats along transects at random site locations across seven vegetation cover types (conifer forest, grasslands,

deciduous shrublands, timber harvests, thins, prescribed fires, and burns). Sites were selected based on a stratified optimal allocation sampling design (Krebs 1999). We classified grasslands, deciduous shrublands, and conifer forests, by using a LANDSAT-derived Montana state landcover map (MTNHP 2017). For harvests, thins, and prescribed fires, we used data from a LANDFIRE disturbance map (LANDFIRE 2017). For burns, we combined data from LANDFIRE and a recent fire perimeter layer made available by Montana Fish, Wildlife & Parks. To determine sampling site locations, we drew random samples within each vegetation cover type using ArcMap 10.6.1. We also used aerial imagery from Google Earth to verify that samples fell within the appropriate vegetation cover type before sampling. We classified the vegetation cover type of sites located in overlapping disturbances (e.g. a harvest overlapping a burn) as the most recent disturbance that occurred there. In total, we sampled vegetation at 884 sites across our study areas during June 1-August 31, 2017-2019 (Table A3).

At each sampling site we established a 40 m transect along the contour of the hillslope. At the 0, 20, and 40m mark on the transect, we recorded plant species composition and visually estimated percent cover of vascular plant species within a $1m^2$ quadrat. Cover estimates for each species were independent of each other, allowing total cover to exceed 100% (since some species overlapped). In the corner of each $1m^2$ quadrat, we established a $0.5m^2$ clip plot and visually estimated percent cover of graminoids, forbs, and shrubs by lifeform within the clip plot. We then clipped all of the aboveground biomass of graminoids, forbs, and shrubs within the clip plot and separated biomass by lifeform into paper bags. We clipped graminoids and forbs 1 cm above the ground to represent the available foraging height of deer. For shrubs, we clipped all leaves and all current annual growth of stems from portions of shrubs that were rooted within the clip plot, less than 2m tall, and not hanging outside of the clip plot. We air-dried biomass samples in

a dry, open space throughout the summer, then oven-dried samples at 50°C in a drying oven for 24 hours in the fall. We then measured dry weight to the nearest hundredth of a gram.

Estimating species-specific plant biomass

We estimated species-specific biomass of every graminoid, forb, and shrub observed in quadrats using linear models based on our clip plot data. For every clip plot, we determined the dry biomass of each lifeform per percent cover of that lifeform. Then, we used multiple linear regression to evaluate percent plant cover, vegetation cover type, tree canopy cover, study area, and interactions between percent plant cover and vegetation cover type as predictors of biomass of each plant lifeform. We square-root transformed biomass and percent cover to improve linearity. We determined the best model for predicting plant biomass based on AIC (Table A4), and applied these models to our species-specific cover data to estimate the biomass of every plant observed in each quadrat. We then filtered our biomass data to forage plants only and calculated the average biomass of forage plants across quadrats at each sampling site to estimate forage biomass (g/m^2) at each sampling site. We determined forage quality ($kcal/m^2$) at each sampling site by multiplying species-specific biomass of forage plants (g/m^2) by species-specific DE (kcal/g).

Developing landscape nutritional models

We developed separate landscape nutritional resources models for predicting forage biomass (g/m^2) and quality ($kcal/m^2$). We used fixed-effects generalized linear models with the log-link, and tested 9 covariates: vegetation cover type, slope, aspect, canopy cover, climatic water deficit (deficit, hereafter) annual forb and graminoid cover (AFG), perennial forb and graminoid cover (PFG), time since disturbance, and study area. We tested for linearity between response variables and independent variables by plotting untransformed and log-transformed versions of

independent variables, and used whichever transformation improved linearity in our final models. We tested interactions between deficit and canopy cover, aspect and canopy cover, a categorical variable combining grasslands and shrublands, and tested for a quadratic effect of slope. We also tested for the effect of canopy cover as both a continuous and categorical (< or ≥40%) variable. On the Rocky Mountain Front, we tested an interaction between grasslands and a categorical variable for low elevation areas (<1700m, the median elevation in that study area), to account for potentially separate vegetation dynamics within the lowland prairie region of that study area and the montane forested region. Deficit is the potential evapotranspiration of a site minus the actual evapotranspiration of a site, and accounts for the effects of both evaporative demand and water availability on a site's water balance (Stephenson 1998). We obtained estimates of deficit at a $30m^2$ resolution based on a model from Holden (2017). PFG and AFG estimates were obtained from the Rangeland Analysis Platform (Jones et al. 2018), which is a spatial model developed trained on 30,000 sampling locations across the western United States that uses Random Forest Modelling to predict percent land cover of plant functional groups across open-canopy cover types at a $30m^2$ resolution. Because the Rangeland Analysis Platform poorly predicts plant cover under high canopy cover, we masked out values in areas with over 40% tree canopy cover. PFG and AFG were sampling season-specific estimates, whereas all other variables represented averages across sampling seasons.

We combined data from across field seasons for developing landscape forage models. To increase our effective sample size, we combined data from the Whitefish Range and Cabinet-Salish study areas, since those study areas overlapped each other and contained similar biotic and climatic conditions. We modeled forage on the Rocky Mountain Front separately, since that study area contained unique vegetation communities (e.g. lowland prairie) and climate

conditions. We calculated the Pearson's correlation coefficient (*r*) for each pair of variables and made sure no variables with $r>0.5$ were included in the same model. We developed global models containing the full suite of covariates. We then screened each global model for uninformative parameters by ranking each variable by level of importance (estimated as the absolute value of β /standard error), then sequentially removed one variable at a time in ascending order of importance (Arnold 2010). If removal of a variable reduced AIC, it was discarded from the model. If removal of a main effect increased AIC, but inclusion of that main effect in an interaction decreased AIC, the main effect and interaction were retained. We repeated this process until no additional variable could be removed without increasing AIC. To further control for multicollinearity, we calculated variance inflation factors (VIFs) for each variable and eliminated variables with VIF>5. This resulted in 4 top-ranked models: A Cabinet-Salish/Whitefish forage biomass model, a Rocky Mountain Front forage biomass model (Table A5), a Cabinet-Salish/Whitefish forage quality model, and a Rocky Mountain Front forage quality model (Table A6). We used coefficients from each top ranked model to predict forage biomass and quality across respective study areas at a $30m^2$ resolution. To keep from extrapolating our models beyond the range of resource values we sampled, we capped resource values used for predictions to their maximum value sampled in each study area. To test the accuracy of our predictions, we performed 10-fold internal cross validation and calculated the cross-validation statistic in program R, and calculated R^2 values for top models.

Forage quality was highest in harvested forests on the Rocky Mountain Front and in the Cabinet-Salish, and was highest in grasslands in the Whitefish Range. Forage quality was lowest in conifer forests across all study areas. The best models for predicting forage quality explained

11.4% of the variation in quality in the Cabinet-Salish and Whitefish Range and 15.3% on the Rocky Mountain Front.

Table A1. Top summer forage taxa in mule deer diets, % diet composition of each taxa by study area, and selection for each forage species. Top forage plants were diet items that made up at least 2% of deer diets by study area, or were selected disproportionately to their available biomass on the landscape.

Study Area	Forage taxa	Lifeform	% Diet	Selection
Cabinet-Salish	*Symphyotrichum spp.*	Forb	0.21	1.94
Cabinet-Salish	*Solidago missouriensis*	Forb	0.21	2.37
Cabinet-Salish	*Epilobium spp.*	Forb	0.28	1.88
Cabinet-Salish	*Heracleum maximum*	Forb	0.28	3.93
Cabinet-Salish	*Angelica spp.*	Forb	0.28	8.18
Cabinet-Salish	*Erigeron spp.*	Forb	0.33	4.39
Cabinet-Salish	*Trifolium spp.*	Forb	0.38	16.11
Cabinet-Salish	*Crataegus spp.*	Shrub	0.39	>100
Cabinet-Salish	*Dasiphora fruticosa*	Shrub	0.41	4.20
Cabinet-Salish	*Crepis spp.*	Forb	0.48	72.66
Cabinet-Salish	*Phleum spp.*	Graminoid	0.69	1.35
Cabinet-Salish	*Potentilla spp.*	Shrub	0.77	12.16
Cabinet-Salish	*Eriogonum spp.*	Forb	0.92	71.54
Cabinet-Salish	*Heuchera spp.*	Forb	1.06	1.01
Cabinet-Salish	*Poa spp.*	Graminoid	1.32	1.42
Cabinet-Salish	*Pascopyrum smithii*	Graminoid	1.36	11.69
Cabinet-Salish	*Elymus spp.*	Graminoid	1.36	>100
Cabinet-Salish	*Medicago spp.*	Forb	1.38	4.25
Cabinet-Salish	*Ribes spp.*	Shrub	2.19	5.65
Cabinet-Salish	*Spiraea spp.*	Shrub	2.44	0.12
Cabinet-Salish	*Bromus spp.*	Graminoid	2.63	0.29
Cabinet-Salish	*Amelanchier alnifolia*	Shrub	3.28	0.40
Cabinet-Salish	*Chamerion angustifolium*	Forb	9.21	2.91
Cabinet-Salish	*Rubus spp.*	Shrub	11.23	3.82
Cabinet-Salish	*Rosa spp.*	Shrub	11.23	8.71
Cabinet-Salish	*Ceanothus spp.*	Shrub	11.78	3.80
Cabinet-Salish	*Fragaria spp.*	Forb	12.73	2.06
Rocky Mtn. Front	*Leucanthemum vulgare*	Forb	0.18	20.62
Rocky Mtn. Front	*Hordeum jubatum*	Graminoid	0.19	11.82
Rocky Mtn. Front	*Ribes spp.*	Shrub	0.41	8.66

Rocky Mtn. Front	*Symphyotrichum spp.*	Forb	0.62	2.18
Rocky Mtn. Front	*Gutierrezia sarothrae*	Shrub	0.62	8.65
Rocky Mtn. Front	*Medicago spp.*	Forb	0.64	1.64
Rocky Mtn. Front	*Potentilla spp.*	Forb	0.68	1.95
Rocky Mtn. Front	*Salix spp.*	Shrub	0.94	2.00
Rocky Mtn. Front	*Trisetum spp.*	Graminoid	1.08	81.77
Rocky Mtn. Front	*Eriogonum umbellatum*	Forb	1.29	1.98
Rocky Mtn. Front	*Hedysarum spp.*	Forb	1.5	>100
Rocky Mtn. Front	*Sphaeralcea coccinea*	Forb	1.72	13.86
Rocky Mtn. Front	*Poa spp.*	Graminoid	1.89	2.12
Rocky Mtn. Front	*Chamerion angustifolium*	Forb	2.16	0.53
Rocky Mtn. Front	*Spiraea spp.*	Shrub	2.23	0.19
Rocky Mtn. Front	*Lactuca spp.*	Forb	2.28	19.61
Rocky Mtn. Front	*Bromus spp.*	Graminoid	3.83	0.24
Rocky Mtn. Front	*Ratibida columnifera*	Forb	4.39	>100
Rocky Mtn. Front	*Rubus spp.*	Shrub	9.1	5.70
Rocky Mtn. Front	*Rosa spp.*	Shrub	13.56	10.78
Rocky Mtn. Front	*Fragaria spp.*	Forb	14.39	2.98
Rocky Mtn. Front	*Plantago spp.*	Forb	15.89	91.72
Whitefish Range	*Lactuca spp.*	Forb	0.21	1.25
Whitefish Range	*Lomatium spp.*	Forb	0.28	1.51
Whitefish Range	*Erigeron spp.*	Forb	0.33	1.17
Whitefish Range	*Trifolium spp.*	Forb	0.38	3.74
Whitefish Range	*Crepis spp.*	Forb	0.48	10.66
Whitefish Range	*Prunus spp.*	Shrub	0.68	52.52
Whitefish Range	*Phleum spp.*	Graminoid	0.69	1.36
Whitefish Range	*Potentilla spp.*	Forb	0.77	1.91
Whitefish Range	*Eriogonum umbellatum*	Forb	0.92	3.47
Whitefish Range	*Heuchera spp.*	Forb	1.06	1.93
Whitefish Range	*Poa spp.*	Graminoid	1.32	3.06
Whitefish Range	*Elymus spp.*	Graminoid	1.36	1.04
Whitefish Range	*Medicago spp.*	Forb	1.38	6.20
Whitefish Range	*Ribes spp.*	Shrub	2.19	2.59
Whitefish Range	*Spiraea spp.*	Shrub	2.44	0.21
Whitefish Range	*Bromus spp.*	Graminoid	2.63	1.01
Whitefish Range	*Rhamnus spp.*	Shrub	2.7	>100
Whitefish Range	*Amelanchier alnifolia*	Shrub	3.28	0.84
Whitefish Range	*Plantago spp.*	Forb	4.45	>100
Whitefish Range	*Chamerion angustifolium*	Forb	9.21	1.04

Whitefish Range	*Rubus spp.*	Shrub	11.23	1.27
Whitefish Range	*Rosa spp.*	Shrub	11.23	3.97
Whitefish Range	*Ceanothus spp.*	Shrub	11.78	8.36
Whitefish Range	*Fragaria spp.*	Forb	12.73	1.80

Table A2. Digestible energy (DE) values in kcal/g for phenological stages of mule deer summer forage taxa, average DE values across phenological stages, and studies where data for DE calculations originated from.

Taxa name	Lifeform	Emergent	Flowering	Fruiting	Mature seed	Senesced	Average	Data source
Chamerion angustifolium	forb	2.22	2.38	2.78			2.54	This study
Epilobium spp.	forb						2.45	Wagoner (2011)
Eriogonum umbellatum	forb						2.6	Wagoner (2011)
Fragaria vesca	forb						2.7	Hull (2018)
Lomatium spp.	forb						2.47	Wagoner (2011)
Bromus spp.	graminoid	3.01	2.98	2.94	2.59	2.67	2.84	Proffitt et al. (2016)
Elymus spp.	graminoid	3.18	2.67	2.61		2.46	2.73	Proffitt et al. (2016)
Phleum spp.	graminoid	3.06	2.74	2.74		2.84	2.84	Proffitt et al. (2016)
Poa spp.	graminoid	3.02	2.81	2.61	2.92	2.59	2.79	Proffitt et al. (2016)
Amelanchier alnifolia	shrub	2.14		2.05			2.08	This study
Ceanothus spp.	shrub						3.26	Hull (2018)
Dasiphora fruticosa	shrub		2.68				2.68	This study
Ribes spp.	shrub	2.58		2.73			2.65	This study
Rosa woodsii	shrub						2.74	Hull (2018)
Rubus spp.	shrub	1.63	1.9	2.51			2.01	This study
Salix spp.	shrub	2.1		1.96			2.07	This study
Spiraea spp.	shrub						3.17	Hull (2018)
Symphoricarpos albus	shrub	2.34	2.55	2.45			2.44	This study

Table A3. Vegetation survey sample size goals determined from power analysis, number of samples achieved, percent area of each study area by landcover type, and mean and SD of forage biomass and quality measured at transects.

Study Area	Landcover type	Sampling goal	Samples achieved	% Study area	Forage biomass (g/m2)		Forage quality (kcal/m2)	
					Mean	SD	Mean	SD
Cabinet / Salish	Conifer forest	32	131	60.63	1.511	1.561	4.255	4.335
	Deciduous shrub	32	24	3.07	3.344	2.858	7.928	7.842
	Grassland	32	35	6.34	2.516	2.694	6.599	7.719
	Harvested forest	32	50	4.46	3.107	2.307	8.365	5.889
	Prescribed fire	32	36	1.55	2.08	1.728	5.671	4.945
	Thin	32	23	4.55	1.608	0.793	4.758	2.288
	Burn	32	26	11.1	3.29	3.229	8.184	7.946
	Total	224	325	91.7	2.245	2.233	6.002	5.907
Whitefish Range	Conifer forest	32	116	59.73	1.645	1.827	4.162	4.505
	Deciduous shrub	32	21	2.62	4.275	4.899	8.676	10.426
	Grassland	32	27	1.99	4.853	5.544	11.901	14.481
	Harvested forest	32	36	2.95	4.082	2.867	10.34	7.272
	Prescribed fire	32	32	0.51	2.37	2.143	6.603	6.039
	Thin	32	15	3.76	2.482	1.302	6.979	3.807
	Burn	32	26	27.04	4.641	4.367	11.474	12.127
	Total	224	273	98.6	2.859	3.249	7.164	8.202
Rocky Mtn. Front	Conifer forest	32	94	41.05	1.619	1.612	4.469	4.87
	Deciduous shrub	32	24	2.9	2.729	3.386	6.619	9.58
	Grassland	32	69	15.2	3.816	5.335	10.032	15.047
	Harvested forest	32	11	0.08	3.831	3.467	11.24	10.339
	Prescribed fire	32	15	1.53	2.544	2.369	7.06	7.041
	Thin	32	2	0.001	6.774	1.631	9.126	12.906
	Burn	32	71	31.23	3.696	3.077	10.142	8.478
	Total	224	286	91.991	2.941	3.497	7.793	9.781
All study areas	Conifer forest	96	341	-	1.586	1.669	4.277	4.525
	Deciduous shrub	96	69	-	3.423	3.774	7.726	9.211
	Grassland	96	131	-	3.617	4.764	9.342	13.157
	Harvested forest	96	97	-	3.561	2.687	9.469	7.051
	Prescribed fire	96	83	-	2.28	2.007	6.289	5.754
	Thin	96	40	-	2.077	1.329	5.809	3.764
	Burn	96	123	-	3.761	3.388	9.891	9.168
	Total	672	884	-	2.649	3.003	6.918	8.011

Table A4. Parameters and coefficients from top models for estimating the square-root of species-specific biomass (in grams) of plants by lifeform.

Lifeform	Parameter	Coefficient	SE	p
Forbs	Intercept	0.341	0.06	< 0.001
	Sqrt (% cover)	0.702	0.011	< 0.001
	% Canopy cover	-0.012	< 0.001	< 0.001
Graminoids	Intercept	0.469	0.048	< 0.001
	Sqrt (% cover)	0.661	0.008	< 0.001
	% Canopy cover	-0.006	< 0.001	< 0.001
	Rocky Mtn. Front	-0.092	0.04	0.022
	Whitefish Range	-0.235	0.04	< 0.001
Shrubs	Intercept	0.351	0.033	< 0.001
	Sqrt (% cover)	0.499	0.006	< 0.001
	% Canopy cover	-0.007	< 0.001	< 0.001

Table A5. Coefficient estimates for top models predicting forage quality in log(kcal/m^2) in the Cabinet-Salish, Whitefish Range, and Rocky Mountain Front in western Montana.

	Cabinet-Salish and Whitefish Range			Rocky Mountain Front		
		Confidence Interval			Confidence Interval	
Covariatea	Estimate	2.50%	97.50%	Estimate	2.50%	97.50%
(Intercept)	1.028	-0.027	2.085	-1.471	-4.718	1.777
Conifer	-0.627	-1.022	-0.233			
Grass/shrubland	-0.557	-1.011	-0.104			
Rx Fire	-0.433	-0.933	0.067			
South	0.636	-0.001	1.273			
Canopy cover	-0.011	-0.023	0.002	-0.015	-0.04	0.009
Deficit	-0.003	0.001	0.005	0.003	-0.002	0.008
[a]AFG	-0.105	-0.163	-0.046	0.191	0.088	0.295
[b]PFG	0.019	0.002	0.036	-0.039	-0.072	-0.006
South * Canopy cover	-0.012	-0.023	-0.001			
Wildfire				1.057	0.113	2.001
Harvest				1.029	-0.706	2.764
Slope				0.145	0.034	0.256
$Slope^2$				-0.003	-0.005	<0.001
Grass/shrubland * Low elevation				-1.717	-3.146	-0.287

[a]AFG: % cover of annual forbs and graminoids.
[b]PFG: % cover of perennial forbs and graminoids.

Table A3. Vegetation survey sample size goals determined from power analysis, number of samples achieved, percent area of each study area by landcover type, and mean and SD of forage biomass and quality measured at transects.

Study Area	Landcover type	Sampling goal	Samples achieved	% Study area	Forage biomass (g/m2)		Forage quality (kcal/m2)	
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Cabinet / Salish	Conifer forest	32	131	60.63	1.511	1.561	4.255	4.335
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	Prescribed fire	32	36	1.55	2.08	1.728	5.671	4.945
	Thin	32	23	4.55	1.608	0.793	4.758	2.288
	Burn	32	26	11.1	3.29	3.229	8.184	7.946
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	Thin	32	2	0.001	6.774	1.631	9.126	12.906
	Burn	32	71	31.23	3.696	3.077	10.142	8.478
	Total	224	286	91.991	2.941	3.497	7.793	9.781
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	Harvested forest	96	97	-	3.561	2.687	9.469	7.051
	Prescribed fire	96	83	-	2.28	2.007	6.289	5.754
	Thin	96	40	-	2.077	1.329	5.809	3.764
	Burn	96	123	-	3.761	3.388	9.891	9.168
	Total	672	884	-	2.649	3.003	6.918	8.011

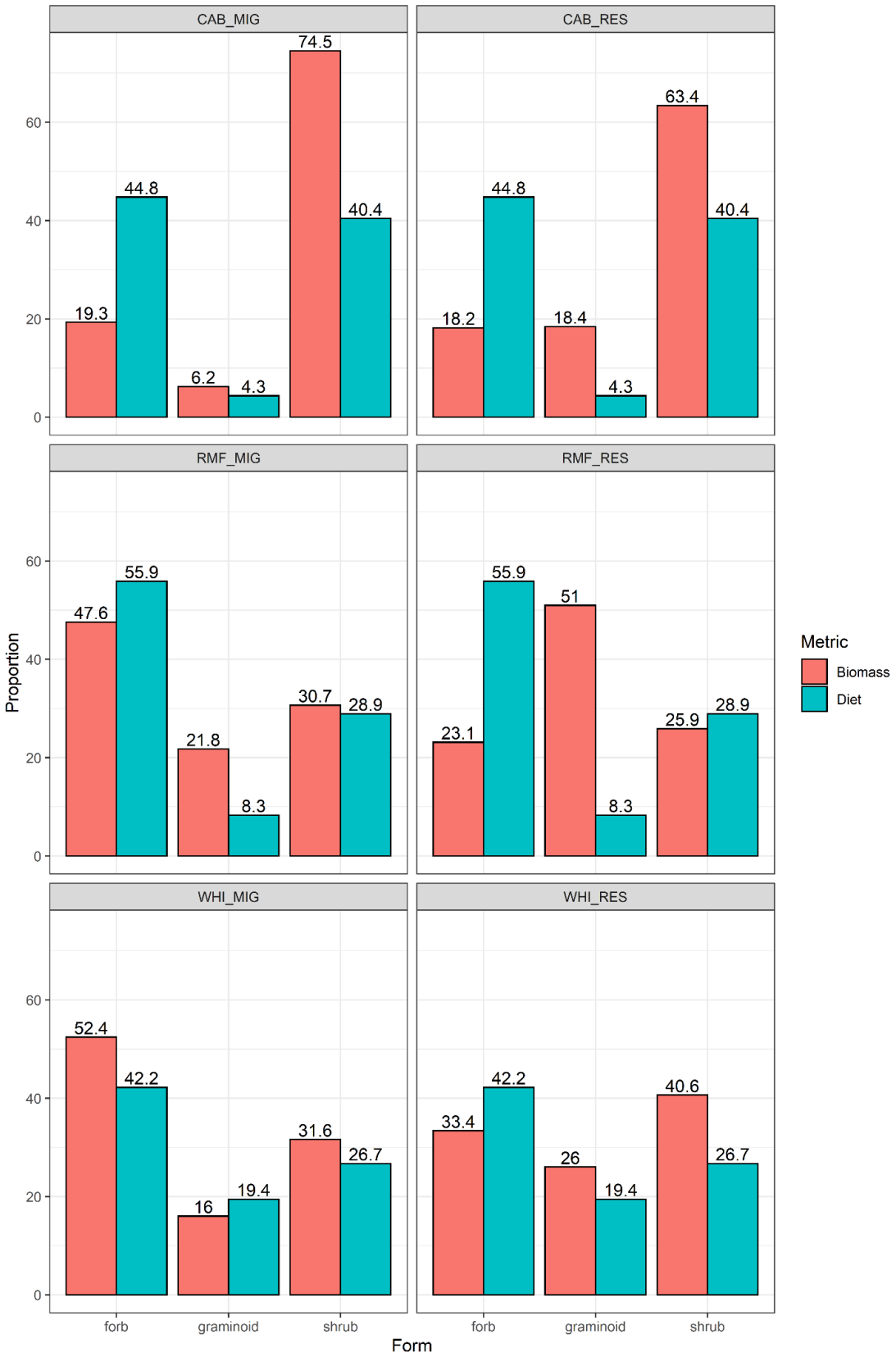

Figure A1. Proportion of forage biomass by plant lifeform (forbs, graminoids, shrubs) in summer ranges of migrants (left column) and residents (right column) in 3 study areas (rows), compared to proportion of those lifeforms in mule deer diets by study area.

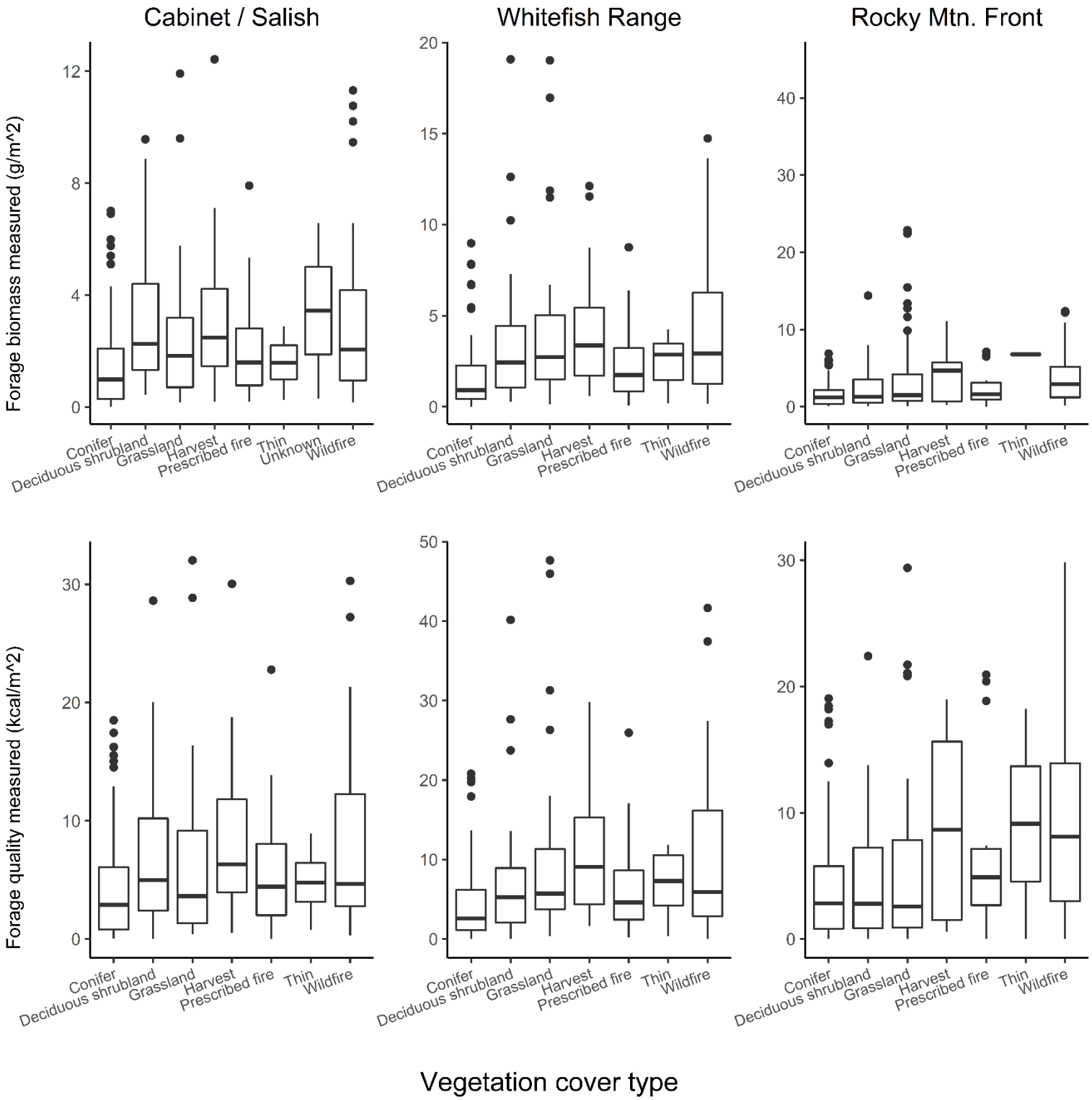

Figure A2. Forage biomass and quality measured at transects across different vegetation cover types and study areas.

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Appendix B.

Modeling probability of GPS collar fixes

Mule deer GPS-collar upload rates to GlobalStar satellites (fix rates) were highly variable. We deployed 121 Lotek LifeCycle 330 collars and 9 Lotek LifeCycle Pro 330 collars. The LifeCycle Pro collars had very low fix rates ranging from 4.8% to 19%, so we chose not to include data from these collars in RSF analysis. Of the remaining 121 Lotek LifeCycle 330 collars deployed, fix rates ranged from 29.98% to 100%. Lower fix rates of some collars may have been a result of habitat-induced biases, which can affect RSF modeling (Frair et al. 2010). We corrected for these biases by developing a spatial model to predict the probability of a collar acquiring a fix (*Pfix*) as a function of habitat variables.

We used data from 9 Lotek LifeCycle 330 collars with store-on-board data that we recovered from deer that died. For each location provided by these collars, we assigned a binary response variable, "Fix", coded as a 1 if the location uploaded to satellites and a 0 if it didn't. The *Pfix* model training dataset contained 6769 fixed locations (1s) and 1890 non-fixed locations (0s). We used logistic regression to estimate *Pfix* using variables known to commonly affect collar fix rates (Frair et al. 2010, Nielson et al. 2009; DeCesare et al. 2012). We screened covariates for collinearity and only included covariates with Pearson correlation coefficients (r) < 0.5 and variance inflation factors (VIF) < 5. We then constructed a global generalized linear model (glm) for *Pfix* that included percent slope, topographic position index (TPI), time of day, cos(aspect), and quadratic effects of slope and time. We used the 'dredge' function from the MuMIN (Barton 2018) package in R to generate a set of models of reasonable combinations of covariates based on the original global model. We ranked models returned by dredge using Akaike's Information Criterion (AIC) (Burnham and Anderson, 2002), then subset models with $\triangle$AIC < 2. We averaged the coefficients of this subset of top models using the 'model.avg' function from MuMIN (Barton 2018). We calculated 95% confidence intervals for coefficients in

this model, and removed variables whose confidence interval overlapped zero to give me a final top model. We conducted internal model validation using the "kxvglm" package (Boyce 2006) in R to perform k-fold cross validation.

Our final *Pfix* model contained TPI and canopy cover as explanatory variables (Table B1). *Pfix* was lower in areas with high canopy cover and within valleys and drainages, and higher on ridgelies and peaks. The model performed well in k-folds cross validation, and mean spearman rank correlation across folds of data was 0.976. We extrapolated this model to every location in our RSF model training dataset and weighted each location by 1/*Pfix* in our final RSF models.

Table B1. Parameters and **c**oefficients (on logit scale) and 95% confidence intervals (CI's) of *Pfix* model for GPS collars.

Parameter	Coefficient	Lower CI	Upper CI	p
Intercept	1.8725	1.776	1.969	<0.001
% Canopy cover	-0.0235	-0.026	-0.021	<0.001
TPI	0.0021	<0.001	-0.004	0.004

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Appendix C.

Classifying Mule Deer Migratory Strategies

Seasonal movement behaviors of mule deer can fall along a spectrum ranging from complete resident strategies to short distant and long distant migrations. We used pre-hoc and post-hoc classification rules to classify individual mule deer summer movement behaviors into either migrant or resident categories using net squared displacement (NSD) (Bunnefeld et al. 2011). NSD measures the straight-line distance between an animal's starting point and subsequent daily locations. We used the migrateR package (Spitz, Hebblewhite, and Stephenson 2017) in Program R version 3.6.1 (R Core Team 2019) to classify movement behaviors. MigrateR fits a set of a-priori non-linear models representing resident, nomadic, dispersal, mixed-migratory, or migratory behaviors to individual animal NSD data, and then compares these models using AIC to determine which model best explains an animal's movement behavior.

We excluded mixed-migrant (migrants that return to a different wintering area) models from consideration in model selection and used post-hoc classification rules to classify these behaviors as either migrant or resident, because we wanted to form more general conclusions regarding contrasts in resource selection behaviors of migrants versus residents. No deer were classified as nomads in this analysis. After identifying the best-supported NSD model of behavior for each individual, we used post-hoc classification rules based on parameter constraints to accommodate the idiosyncratic behaviors of mule deer in our study. MigrateR relies on model parameters δ, representing the square of the distance separating winter and summer ranges, t, the time since departing winter range, θ, the midpoint of departing movement, ϕ, the time required to complete ½ to ¾ of the migration to summer range, and ρ, the length of time spent on summer range.

We defined migrants as animals that moved at least 9 km ($\delta > 81$) between ranges prior to the end of summer ($t < 240$ days since start point). We observed individuals remaining on

summer range from early May – late December of a single year, thus, we adjusted ρ to allow migrants to remain on summer range for up to 240 days. We defined residents as animals that moved less than 9 km between seasonal ranges. Thus, we classified animals as resident if their best-supported model indicated they "dispersed" or "migrated" less than 9 km.

The Rocky Mountain Front had the highest proportion of residents and the Whitefish Range had the lowest. There was 1 disperser on the Rocky Mountain Front. In spring of 2017, this deer travelled 31.49 km from its winter home range to a new home range, and never left this home range by the time monitoring ended in Fall 2019, so we re-classified this deer as a resident. Across study areas, the average straight-line distance between winter and summer home range centers was 26.20 km (SD = 12.20), and ranged from 7.43 km to 58.30 km (Table C1).

Table C1. Number of collared mule deer does that were analyzed in summer RSFs and numbers and proportions of migrants and residents in analyzed sample with summaries of migration distances.

Study Area	Collared individuals analyzed	Migrants		Residents		Distance between winter and summer home range centers of migrants (km)			
		n	%	n	%	Mean	SD	Min	Max
Cabinet / Salish	34	27	79.4	7	20.6	33	8.02	20.87	49.07
Rocky Mtn. Front	44	34	77.3	10	22.7	24.09	19.42	7.43	58.3
Whitefish Range	32	27	84.4	5	15.6	23.24	21.71	11.49	44.95
Total	110	88	80	22	20	26.2	12.2	7.43	58.3

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